

POPULATION DYNAMICS AND FISHERY  
MANAGEMENT OF THE ABALONE, *HALIOTIS IRIS*

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## ABSTRACT

The dynamics of an unfished population of the abalone *Haliotis iris* Martyn in Peraki Bay, Banks Peninsula, were studied from 1973 to 1976 and the population parameters interpreted with respect to exploitation of the species.

As *Haliotis iris* cannot yet be aged, a size-class population model was developed along the lines of the Leslie (1945, 1948) matrix model. The population projection matrix incorporates mortality, recruitment and individual growth components, and operates on a population divided into size classes.

The number of animals in the study population, and its size structure, were determined using transects and a stratified random sampling design. In February 1976 the population consisted of about 179 000 animals on 4.5 km of coastline, and the length frequency distribution was strongly skewed to the left, indicating an accumulation of old individuals and a recent history of low recruitment.

Growth of animals < 70 mm long was determined from changes in length frequency, and of larger animals by the analysis of tag returns. Equations which incorporate individual variability of growth parameters were developed for the analysis of tag return data. The mean parameters of the Von Bertalanffy growth equation for the study population are  $K = 0.1636$  and  $L = 131.9$  mm. Both are lower than those reported for abalones in a more typical habitat near Kaikoura, probably because of

differences in the availability and quality of algal food species.

Annual instantaneous natural mortality, as estimated by several methods from population size structure and individual growth rate data, is about 0.1, suggesting that some individuals live in excess of 30 years. The main cause of death is burial by sand during storms.

The reproductive cycle was examined. *H. iris* failed to spawn during 2 of the 4 years monitored and the failure during one year was geographically widespread. Egg production per female in the study area increases with body length up to a maximum of 1-2 million in 115-130 mm individuals; whereas at Kaikoura it continues to increase with length and reaches 11 million per 150 mm female.

Recruitment, as estimated from population sampling, was 2000-5000 two year olds per year and seemed independent of local spawning success. Surface current systems could transport planktonic *H. iris* larvae far from a parent stock. Simulations, using the model developed, suggest that the population size structure in February 1976 resulted from a short (about 5 year) period of high recruitment, followed by 10-15 years of low recruitment.

The present minimum legal size for the fishery (127 mm) provides close to the maximum yield per recruitment for most stocks, although some local reductions could be warranted where individual growth rate and asymptotic size are low or where the natural mortality is greater than 0.15.

## GENERAL INTRODUCTION

The New Zealand abalone or paua, *Haliotis iris* Martyn, is a large (up to about 180 mm) mollusc found in the sublittoral fringe and subtidally on hard substrates. It is discontinuously distributed along the coasts of both main islands of New Zealand and of the Chatham, Stewart and Snares Islands. Two other haliotid species, *H. australis* and *H. virginea* (divided into four subspecies, see Poore, 1969), are also found in New Zealand. They are smaller (maximum length about 90 mm and 70 mm respectively) than *H. iris* and less common.

Although the genus is concentrated mainly in the Pacific Basin (both in numbers and species), it has a worldwide distribution and comprises about 130 species and subspecies (Cox, 1962). Individual species have a geographical range of up to a few thousand kilometres.

The higher taxonomy of *Haliotis*, as applied by Morton (1963), is:

Phylum: Mollusca

Class: Gastropoda

Subclass: Prosobranchia

Order: Archaeogastropoda

Superfamily: Zeugobranchia

Family: Haliotidae                      Rafinesque, 1815

Genus: *Haliotis*                      Linnaeus, 1758

As prosobranch gastropods, haliotids have a single shell and have lost the ancestral bilateral symmetry as a result of torsion, which caused the ctenidia (gills), anus and mantle cavity to lie anteriorly. All members of the superfamily Zeugobranchia, the most primitive archaeogastropods, have a slit in the mantle with a corresponding slit or series of perforations (as in *Haliotis*) in the shell, through which flows the exhalant water current. The anatomy of *Haliotis* has been described in detail by Crofts (1929) and Cox (1962).

Haliotids' shells are easily recognised by the very large aperture, relative to shell depth. The whole shell consists mainly of the last whorl (see Fig. 6.2).

Work on haliotids has been extensive, and includes detailed anatomical studies (e.g. Crofts, 1929), ecological studies (e.g. Cox, 1962; Shepherd, 1973a) and work on larval development (e.g. Ino, 1952).

Poore (1969, 1972a, b, c, d) described the general biology of *H. iris* at Kaikoura (see Fig. 2.1), including feeding, movement, growth, reproduction and larval development. The only other publications on *H. iris* are on its general ecology (Sinclair, 1963), feeding (Tunbridge, 1967) and body proportions (Cleaver, 1966).

*H. iris* are found under boulders, in crevices and on open rock faces, from the intertidal zone to a depth of about 20 metres. They feed on both drifting and attached marine algae, which are held beneath the foot and broken up by the radula.



*H. iris* is sedentary and apparently does not possess a 'homing' behaviour (i.e. individuals do not have a specific home site to which they return after feeding or other excursions). The sexes are separate, and spawning (which occurs in the late summer or autumn) may fail in some years. Fertilization is external, and development passes through free-swimming trochophore and veliger stages. Larval *H. iris* are planktonic for 5-10 days, then settle (probably on to a hard substrate) to begin benthic life. It is likely that the settlement site is selected during a 'creeping stage' (Crofts, 1937), which may be benthic for a time, but can return to the plankton if conditions prove to be unsuitable for settlement. Young abalone live predominantly under boulders between the sublittoral fringe and a depth of about 5 m, and probably feed in the algal film and small pieces of drift algae. They remain under boulders until they are about 70 mm in length, after which they are found throughout the full habitat range of the species.

Much of the impetus for research on abalones results from their commercial exploitation (particularly intense in California, South Africa, Japan and Australia) and the need to devise legislation, both to protect the stocks and to obtain the best yield from them. However, despite the considerable data available concerning some aspects of the biology of abalones (notably growth, reproduction and feeding), the effects of various management strategies on the yield obtainable have not been determined. The two main reasons for this are:

i) Abalones in the complex sublittoral habitat are very difficult to tag, relocate and sample reliably (see Cox, 1962), with the result that there is little data on natural mortality and stock size.

ii) The methods used to examine the effects of various combinations of minimum legal size and fishing mortality on the yield obtained from a fishery (see Beverton and Holt, 1957; Ricker, 1958) require that the exploited species can be aged, but there is no reliable method of age determination for most commercial abalone species (see Cox, 1962; Poore, 1972c). The exceptions are *H. discus hannai* and *H. tuberculata* (see Sakai, 1960, and Forster, 1967, respectively), but the fisheries for these species have not been examined.

All three New Zealand haliotids, and particularly *H. iris*, have been exploited by man for many hundreds of years. The Maoris used paua for food, and the shell featured prominently in traditional Maori carvings (Phillips, 1935). Maori fishing probably had little effect on the populations because it is unlikely that fishermen had access to the bulk of the adult stock, which occurs at depths of from one to twenty metres. Even during the early 1900's, about one hundred years after the arrival of Europeans in New Zealand, the paua stocks were not heavily fished. The New Zealand abalone was considered unappetizing because of its black epidermis, and was not taken commercially until a bleaching method was developed. Following this an export market developed, and since the late 1960's *H. iris* has supported a rapidly expanding

commercial fishery. The other New Zealand haliotid species are too small and rare to be taken commercially.

The total annual commercial abalone catches for the years 1962 to 1975 are given in Table I. No data are available concerning the catch taken by amateur fishermen. Commercial catch and effort statistics for the main fishing areas are given by Cooper (1976), and show a rapid decline in landings during 1974 and 1975 following the depletion of dense beds of old animals between 1970 and 1973. The effects of this decline on the total catches for 1974 and 1975 were masked to some extent by the large catches obtained in these years from intensive exploitation of previously unfished stocks along the Southland-Stewart Island coast. Catches in future will probably decline as fewer unfished stocks are discovered and currently-exploited abalone beds become reduced.

Table I. Commercial catches of *H. iris* extracted from Ministry of Agriculture and Fisheries annual reports

Year	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Catch (tonnes)	26	15	45	24	25	59	64	443	588	1461	714	813	439	600

The present regulations relating to the taking of *H. iris* are:

Minimum legal size: 127 mm.

Maximum quantity: One tonne per licence holder per week (commercial), and 10 animals per person per day to a maximum of 50 for a group of 5 people (amateur).

Collection: Underwater breathing apparatus must not be used and the catch must be landed alive in the shell.

Licensing: The fishery is unrestricted in that any number of fishing licences may be issued, and a licence holder may operate in any part of New Zealand (within the limits imposed upon fishing activities by other legislation, e.g. the Marine Reserves Act and Department of Health directives).

This study was undertaken in an attempt to aid management of the *H. iris* fishery, and had two aims:

i) to estimate the parameters of an *H. iris* population (i.e. mortality rate, reproduction, recruitment, population size and structure, and individual growth rates), and

ii) to use these estimates to determine the minimum legal size which results in the 'best' use of the resource.

The first obstacle encountered was the absence of theoretical procedures for examining the exploitation of a species which cannot be adequately aged. Thus, in Chapter 1, a size class population simulation model is developed.

A model in this context was defined by Shannon (1975) as '... a representation of a group of objects of ideas in some form other than the entity itself.' Shannon then defined simulation as 'the process of designing a model of a real system and conducting experiments with this model for the purpose of understanding the behaviour of the system

or evaluating various strategies (within the limits imposed by a ... set of criteria) for the operation of the system'. Thus simulation may be used to determine the consequences of the set of hypotheses embodied in a model, and, ideally the consequences would then be tested against the behaviour of the real system. The concept of modelling is basic to scientific methodology, and, to quote Rutter (1971), 'we discover at the outset that we have been building models all our lives'. A population simulation model is not presumed to be a complete description of the population and its environment. The model is an attempt to approximate the main population processes which are relevant to the objects of the study and must be a simplification of nature so as to remain manageable in terms of the data and computation required for its application.

The model presented in Chapter 1 was developed from general consideration of exploited populations and does not relate specifically to abalone. Verification of the model was not attempted, since this in itself would require a detailed and time-consuming study programme, and the broad aims of this study demanded a high level of time commitment to model development and collection of data in the field.

The parameter estimates and biological framework required for application of the population model to *H. iris* are given in Chapters 2 to 6 inclusive. These include estimates of the natural mortality rate, population number and size structure, reproductive cycle, recruitment and growth rate. In Chapter 7 the population model is used to

find an historical pattern of recruitment which could have resulted in the observed population size structure, and to examine the fishery in terms of the yield per recruit.

# 1. A SIZE CLASS MATRIX MODEL FOR AN EXPLOITED FISH POPULATION

## 1.1 INTRODUCTION

Fishery harvesting models have developed along two main lines - one treating the fished population as a single, unstructured unit, and the other considering it to be made up of a number of age classes. Unstructured models (or surplus production models) assume that the population growth rate is related by some simple, known function to the current population size. Very little information on the species concerned is required, generally only catch and effort data for a series of years. This approach to fisheries analysis was used initially by Graham (1935, 1939), but Schaefer (1954, 1957) presented the linear surplus production model in its presently used form. More recent extensions and generalisations of the model have been published by Ricker (1958), Pella and Tomlinson (1969), and Fox (1970, 1975). Structured or 'dynamic pool' models, in which the biological parameters of growth and mortality are applied to the population recruitment, form the second major type of model. Usually provision for age-specific variation in the parameters is made, and by varying the magnitude of a fishing mortality term and the age of fish it affects, the effect on the population of various fishing regimes may be investigated.

When an estimate of recruitment is not available it may be set at some arbitrary, constant level and the model solved for the yield per recruit instead of the total yield from the population. Providing the parameters remain constant over the range of population densities and structures likely to be encountered in the fishery, changes in the yield per recruit reflect the relative effects on the catch of different fishing policies.

Early structured models were described by Beverton and Holt (1957) and Ricker (1958). Besides requiring that it be possible to age the species in question, these models are difficult to apply to non-equilibrium situations, or to species showing marked age specific or seasonal changes in their population parameters. Later dynamic pool models, e.g. Jones and Hall (1972), Southward (1968), Walters (1969), Paulik, Hourston and Larkin (1967), Larkin and McDonald (1969), have become more flexible, and rely on computer simulation rather than analytic solution of the model.

The use of a matrix as a structured population model was introduced by Lewis (1942) and then developed more fully by Leslie (1945, 1948). The population at time  $T$  is represented by a population vector,  $N_T$ , each element ( $n_i$ ,  $i = 1$  to  $Z$ ) being the number of animals present between the ages  $(i-1)$  and  $i$ . The population vector at  $T + t$  is calculated by multiplication of  $N_T$  by a population projection matrix,  $A_t$ , embodying the parameters of survival and fecundity during the period  $t$ .  $A_t$  is a square matrix of order  $z$  (longevity =  $zt$ ) with



$$\begin{aligned}
 a_{1,i} &= f(i) & i = 1, 2, \dots, z \\
 a_{i+1,i} &= S(i) & i = 1, 2, \dots, z-1
 \end{aligned}$$

$f(i)$  is the number of offspring produced during the interval  $t$  per animal of age class  $i$  which survive to be in the first age class at the end of that interval.

$S(i)$  is the proportion of animals in age class  $i$  at time  $T$  surviving to age class  $(i + 1)$  during the interval  $t$ .

The development and application of this kind of model have been reviewed by Usher (1971), and the utility of its application stressed by Paulik (1972). Both Lefkovitch (1965) and Usher (1971) have suggested modifications of the Leslie matrix which allow the use of life cycle stages and size classes respectively. Usher's model of tree populations in a forest required that the trees grew a maximum of one size class per time interval. Although this requirement places severe limits on the model's application to animal populations, Pip and Stewart (1975) have described a means of estimating the parameters of Usher's model from changes in a population's size structure during short time intervals. Lefkovitch (1965) modelled arthropod populations grouped by life cycle stage. Each element of his projection matrix,  $m_{i,j}$ , related the number of animals in the  $i$ th stage at time  $T+t$  to the number in the  $j$ th stage at time  $T$ . He estimated values for these elements by multiple regression analysis. This essentially empirical approach has limitations in that the population's response to changes in the population parameters cannot be directly examined, and has been

criticised by Doubleday (1975).

This chapter presents the general form of a size class projection matrix for constant or density dependent parameters, and describes the use of matrix models in investigating management policies for a fishery.

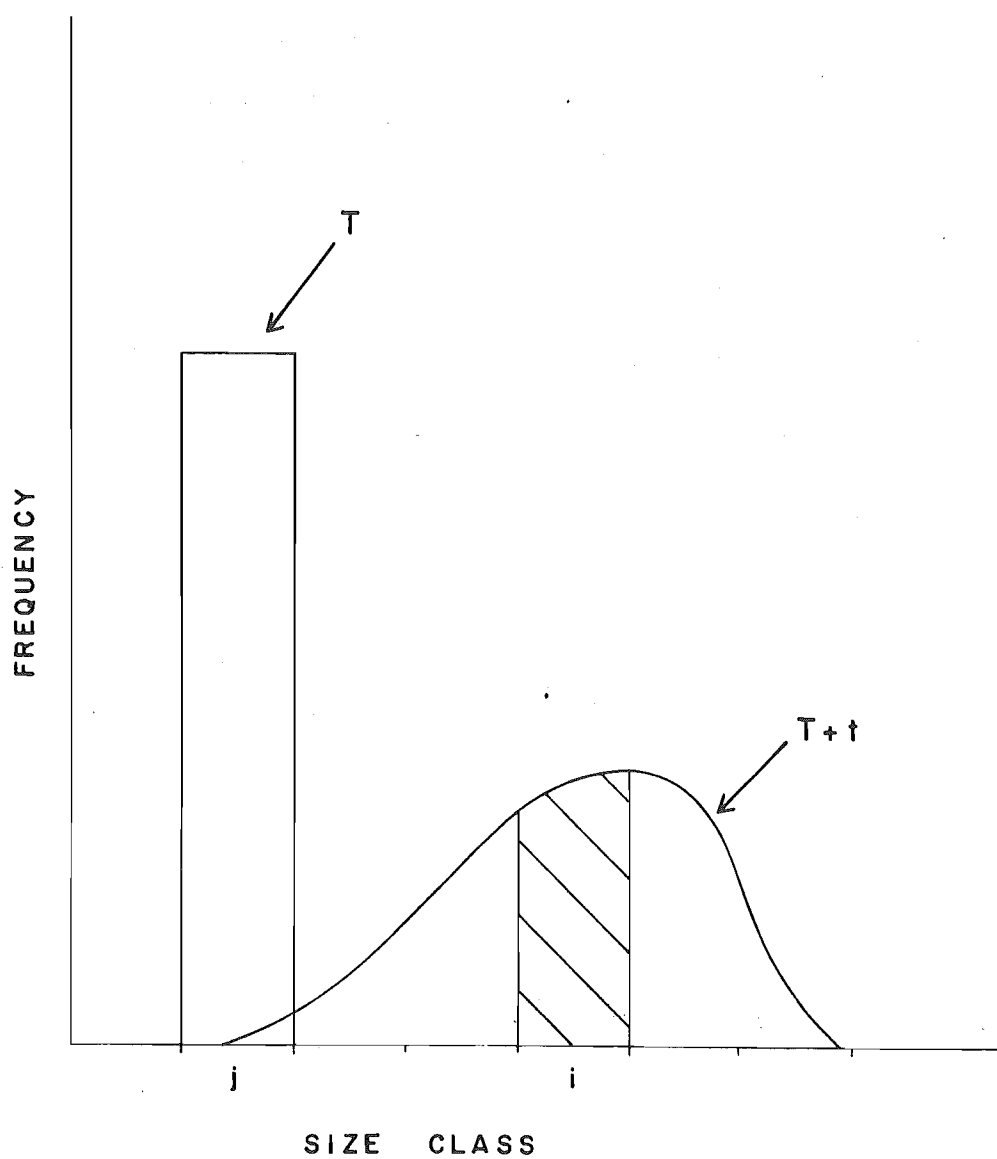
## 1.2 SIZE CLASS PROJECTION MATRIX

A projection matrix is required which will operate on a population vector whose elements are the numbers of animals in each size class. The growth process may be modelled by a square matrix of elements  $P_{i,j}$  that are the proportions of animals in size class  $j$  at time  $T$  which will grow to be in size class  $i$  at time  $T + t$ . Each  $P_{i,j}$  is related to the size specific growth increment by considering the fate of the animals in any source class  $j$  at time  $T$ . Over the period  $t$ , animals initially of mean size  $\bar{I}_j$  will grow by an average increment  $\bar{I}_j$  which will be some function of initial size.

Size may be defined in any convenient terms for a particular species, and the size classes need not all be of the same width. Similarly, there is no restriction on the function used to relate the mean growth increment to the initial size.

The growth increment will show individual variation, so that at time  $T + t$  animals from class  $j$  will form some frequency distribution (Fig. 1.1).  $P_{i,j}$  is the proportion of the total area under this frequency distribution bounded by the class limits of  $i$ .

Figure 1.1 The effect of growth over a period  $t$  on the frequency distribution of animals initially in source size class  $j$ . The shaded area as a proportion of the total area under the  $T + t$  curve is the probability of an animal from class  $j$  at  $T$  being in class  $i$  at  $T + t$ .



The nature of this frequency distribution will depend upon the initial distribution within class  $j$ , the mean increment of the animals from  $j$ , and the distribution which describes individual variability of growth increment. If the size classes are small, the initial distribution of lengths within each class will be approximately uniform and the mean initial length will be the mid-point of the source size class ( $\hat{l}_j$ ).

There are several possible methods of incorporating individual variation into a growth function. Possibly the simplest is to add a random variable to the function. However, a more versatile approach is to consider the parameters of the growth function to differ between individuals and to estimate this variability. Thus, if growth is considered to be described by the Von Bertalanffy (1938) growth equation, the growth increment during time  $t$  of the  $m$ th animal initially in size class  $j$  is

$$I_m = (L_m - l_m) (1 - e^{-K_m t}) \quad (1)$$

where  $L_m$  and  $K_m$  are the Von Bertalanffy growth parameters for the  $m$ th animal.

As shown in Appendix 1.1, the mean length at time  $T + t$  of the group of animals initially in size class  $j$  is

$$E[l_{T+t}] = (E[L_m] - \hat{l}_j) (1 - E[e^{-K_m t}]) + \hat{l}_j \quad (2)$$

and the variance is

$$V[l_{T+t}] = \frac{h_j^2}{12} \{E[e^{-K_m t}]^2 + V[e^{-K_m t}]\} + k_1 V[L_m] + k_2 (E[L_m] - \hat{l}_j)^2 \quad (3)$$

where  $h_j$  is the width of size class  $j$ ;  $k_1$  and  $k_2$  are

functions of  $E[e^{-K_m t}]$ ,  $V[e^{-K_m t}]$  and  $t$  (given in Appendix 1.1). The mean and variance of  $L_m$  and  $e^{-K_m t}$  may be specific to each size class. Further development of equations (2) and (3) is necessary for the model's application to a specific population, and this requires a more detailed examination of the distributions of  $K_m$  and  $L_m$ . Such development is provided in Appendix 3.2, and a method of parameter estimation is given in Appendix 3.3. Although the details provided in these appendices are not relevant to the general description of the population model provided here, it should be noted that it becomes convenient, for the purposes of estimation, to assume that the mean and variance of  $L_m$  and  $e^{-K_m t}$  do not alter with length.

It appears that for many species the growth increment is approximately normally distributed for a given initial length (e.g. Manzer and Taylor, 1947, for lemon sole; Poore, 1972c, for abalones; Burnett, 1969, for eels; Hopkins, 1967, for freshwater crayfish; Feare, 1970, for dogwhelks). When this is the case the length frequency distribution at time  $T + t$  may also be treated as normal, with parameters defined by equations (2) and (3). Each  $P_{i,j}$  is obtained from the areas under a normal curve.

The assumption of Von Bertalanffy growth is by no means essential to application of the model. Any function which fits the available data may be used to relate the growth increment and initial length. A linear relation will be sufficient for most cases as it is necessary only that the parameters remain constant within each size class. Similarly, any integrable function may be used to describe

individual variability in I.

To include mortality in the size class projection matrix, allowance must be made for animals growing through several size classes during the interval  $t$ , each of which could be characterised by a different mortality rate. Each  $P_{i,j}$  is multiplied by a survival,  $S_{i,j}$ , which is the proportion surviving growth from class  $j$  to class  $i$  in time  $t$ . A shorter length of time,  $\Delta t_k$  ( $j \leq k \leq i$ ) is spent in each of the size classes  $j$  to  $i$  inclusive. Thus, using  $M_k$  and  $F_k$  as the instantaneous natural and fishing mortalities respectively in class  $k$ ,  $S_{i,j}$  is

$$S_{i,j} = \exp - [(M_j + F_j)\Delta t_j + (M_{j+1} + F_{j+1})\Delta t_{j+1} + \dots \\ \dots + (M_{i-1} + F_{i-1})\Delta t_{i-1} + (M_i + F_i)\Delta t_i] \quad (4)$$

Normally it will be sufficient to take the time spent in each size class as being proportional to the amount of growth required to pass through that size class, i.e. that over the size range and time interval in question, growth is approximately uniform. So, for size classes of equal width we have

$$\begin{aligned} \text{if } i = j \quad \Delta t_k &= t \quad k = i = j \\ \text{if } i \neq j \quad \Delta t_k &= \frac{t}{2(i-j)} \quad k = j \quad \text{or} \quad k = i \\ \text{and} \quad \Delta t_k &= \frac{t}{(i-j)} \quad j < k < i \end{aligned}$$

If it is thought necessary, a more exact expression for the time spent in each size class may be derived from the size-specific growth function used and the size class

widths. However, simulations using the Von Bertalanffy relationship suggest that this is unnecessary and the inaccuracies involved in partitioning  $t$  as shown above are extremely small, even when growth and mortality rates alter quite markedly with size.

In following the fate of the animals from source size class  $j$  over the interval of time  $t$  the number of deaths may be calculated, and of these deaths the proportion  $F/(F+M)$  is taken by the fishery. This yield will be distributed among all the size classes the animals from class  $j$  pass through or reach during the interval  $t$ .

A yield matrix,  $\underline{Y}$ , may be formed, which when multiplied by any population vector will give a vector of the size (class) specific yield from the population during the interval  $t$ . Each element of this matrix,  $y_{i,j}$ , is the proportion of animals in class  $j$  at time  $T$  which will be caught in class  $i$  during the interval  $t$ .

If the animals do not exhibit negative growth, then

$$y_{i,j} = \frac{F_i}{F_i + M_i} \sum_{r=i}^{r=z} P_{r,j} \exp - [(M_j + F_j) \Delta t_j + (M_{j+1} + F_{j+1}) \Delta t_{j+1} \dots$$

$$\dots + (M_{i-1} + F_{i-1}) \Delta t_{i-1}] (1 - \exp - (M_i + F_i) \Delta t_i) \quad (5)$$

where  $i \geq j$  and  $z$  is the order of the matrix. The first exponential term in equation (5) gives the proportion of animals growing from  $j$  to  $r$  ( $i \leq r \leq z$ ) which survive to enter class  $i$ . The second exponential term gives the proportion of those animals entering class  $i$  which die while in that class. Notice that the  $\Delta t_k$  ( $j \leq k \leq r$ ) terms will be different for each value of  $r$ , as they refer to the



time spent in the  $k$ th size class for animals growing from class  $j$  to  $r$  in time  $t$  (the additional subscript,  $r$ , has been dropped for ease of notation). Equation (5) may easily be extended to include negative growth.

The total number of animals caught in the  $i$ th size class during time interval  $t$  from population vector  $N_T$  is

$$\sum_{l=1}^{l=i} y_{i,l} n_l \quad (6)$$

If the species concerned exhibits negative growth (some  $P_{i,j} \neq 0$  for  $i < j$ )  $l$  must take values from 1 to  $z$ . The yield in numbers may be converted to yield in weight by including a term for size specific weight.

If  $f_i$  is the number of young produced per animal of size class  $i$  during the interval  $t$  which survive to be in size class 1 at the end of that period, the size class projection matrix ( $A_t$ ), for non-negative growth has the form

$$\begin{bmatrix} P_{1,1} S_{1,1} + f_1 & f_2 & f_3 & \dots & f_z \\ P_{2,1} S_{2,1} & P_{2,2} S_{2,2} & 0 & \dots & 0 \\ P_{3,1} S_{3,1} & P_{3,2} S_{3,2} & P_{3,3} S_{3,3} & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ P_{z,1} S_{z,1} & P_{z,2} S_{z,2} & P_{z,3} S_{z,3} & \dots & P_{z,z} S_{z,z} \end{bmatrix} \quad (7)$$

This projection matrix can be extended to model negative growth, and delays in recruitment or partial recruitment may be included by the introduction of 'dummy' size classes.

Recruitment into several size classes (rather than just the first) is modelled by including 'fecundity' terms, similar to those shown, into the relevant rows of the projection matrix.

The population vector at time  $T + t$  is calculated by multiplying the population vector at time  $T$  by the projection matrix

$$\tilde{N}_{T+t} = \tilde{A}_t \tilde{N}_T \quad (8)$$

and for  $k$  such intervals of time

$$\tilde{N}_{T+kt} = \tilde{A}_t^k \tilde{N}_T \quad (9)$$

If the population parameters are different for each of the  $k$  time intervals, the projection matrix for each interval will also be different. These matrices may be pre-multiplied to give a single projection matrix for the time interval  $kt$ . That is,

$$\tilde{A}_{kt} = (\tilde{A}_k \tilde{A}_{k-1} \dots \tilde{A}_1) \quad (10)$$

where period 1 occurs before period 2. And so

$$\tilde{N}_{T+kt} = \tilde{A}_{kt} \tilde{N}_T \quad (11)$$

In a series of premultiplied size class projection matrices, the time interval covered by each matrix need not be the same. Thus a population may be simulated in detail during periods of rapid change without affecting the treatment of periods of more gradual change.

Equations (8), (9) and (11) provide the means of iteratively following the fate of a population, while (10) produces a single projection matrix for a population whose

parameters vary cyclically. For example, if growth, recruitment or mortality differ seasonally (but in the same way each year), equation (10) will give one annual projection matrix which encompasses these differences.

Leslie (1945) has shown for the age class projection matrix that if the elements of the matrix remain fixed then the population will stabilise. That is, the proportion of the population in each age class becomes fixed and the total number of animals in the population changes by a constant proportion during each time period (i.e. the population changes exponentially).

If  $\tilde{V}$  is a vector made up of the proportions of the population in each age class at stability, and  $\lambda_1$  is the population growth rate at stability, then

$$A_t \tilde{V} = \lambda_1 \tilde{V} \quad (12)$$

where  $\lambda_1$  is the dominant eigenvalue and  $\tilde{V}$  is the associated eigenvector (scaled to sum to one) of the projection matrix  $A_t$  (Gantmakher, 1959; Searle, 1966; Usher, 1971).

As shown in Appendix 1.2, a unique, biologically meaningful solution to equation 12 also exists for the size class projection matrix, provided certain reasonable conditions are met (see Appendix 1.2). The eigenvector in this case is made up of the proportions of the population in each size class at stability.

### 1.3 DENSITY DEPENDENCE

The concept of a stable population is applicable only in a temporally constant, unrestricted environment,

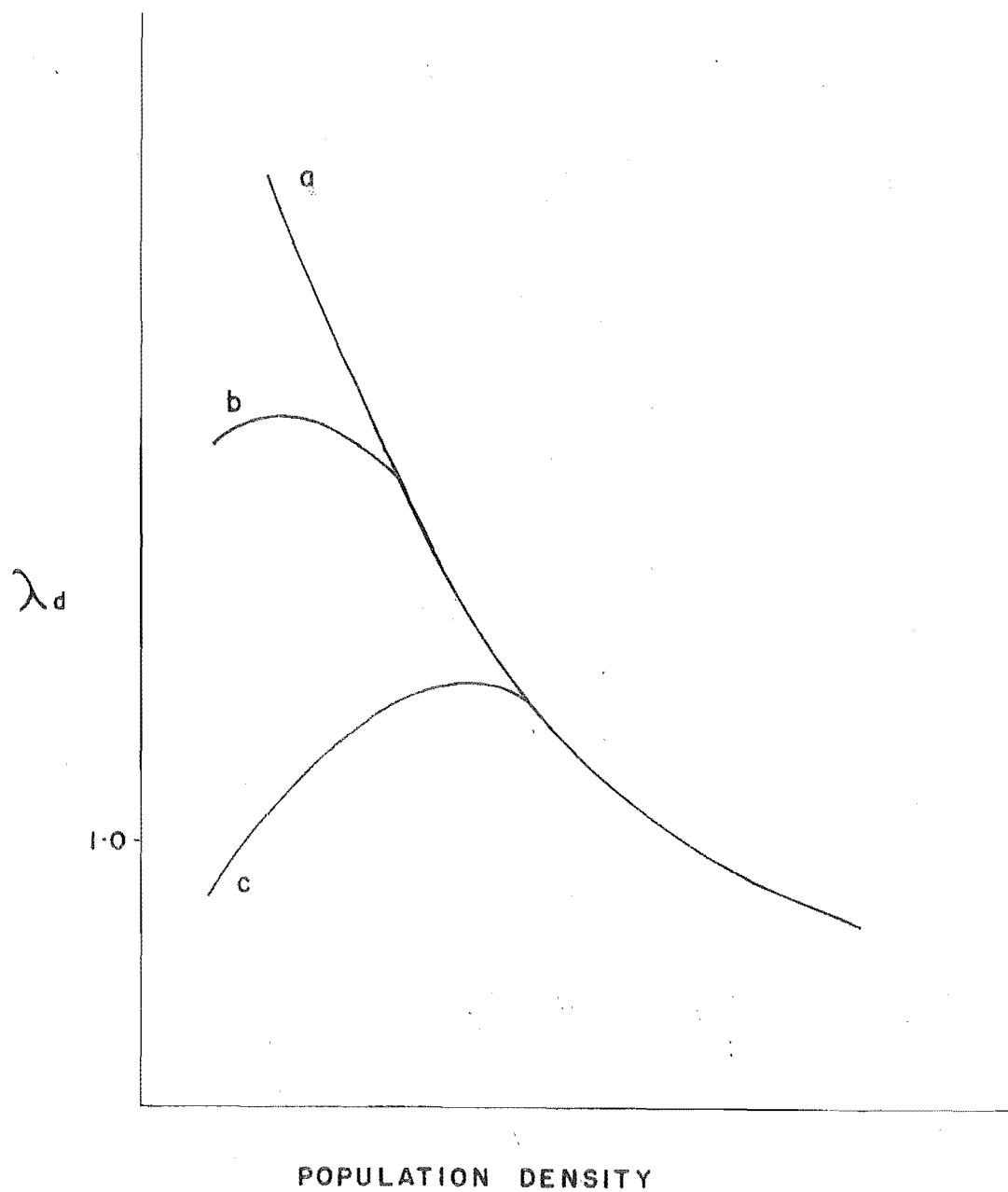
and such a population is predicted to become either infinitely large, zero or remain exactly the same for  $\lambda_1 > 1$ ,  $\lambda_1 < 1$  and  $\lambda_1 = 1$  respectively. More realistically, the population parameters can be expected to alter with population density and changes in the physical environment.

Population density, for most purposes, may be treated as a scalar and defined as some function of the elements of the population vector. (The unit of area is implicitly defined by the area occupied by the population in question.) Examples are the total number of animals in the population, the population biomass or the number of animals within certain size limits.

When the population parameters are taken to be functions of population density, the projection matrix and the solutions to equation (12) may also alter with density. At each density ( $d$ ) there is a specific projection matrix, dominant eigenvalue ( $\lambda_{1d}$ ) and associated eigenvector ( $\vec{V}_d$ ). These refer to the growth rate and structure of the population if it reached stability at density  $d$ . By solving for  $\lambda_{1d}$  over a range of densities, the relationship between  $\lambda_{1d}$  and the population density is established (Beddington, 1974; Smith, 1974). This requires that the relationship between the population parameters and population density be known. Several possible stock-recruitment curves have been published (Beverton and Holt (1957), Ricker (1958), Larkin, Raleigh and Wilimovski (1964), Cushing and Harris (1973), Larkin (1973)), and the density dependence of growth and mortality are discussed by Beverton and Holt (1957).

The relationship between  $\lambda_{1d}$  and density may take a

Figure 1.2 Some possible relationships between population growth rate ( $\lambda_d$ ) and population density.



wide variety of forms for different species because it is determined by the particular functions relating the population parameters of that species to population density. For example, it is conceivable that the relationship is polymodal. However, one would generally expect the relationship between  $\lambda_{1d}$  and population density to be of a form shown in Fig. 1.2. Curve a, a decreasing function of density, would result if mortality increases and individual growth rates and recruitment decrease with population density. If recruitment and growth rates decrease and mortality increases at low population densities (depensatory mortality) a curve of type b would result. Curve c implies that at low population densities recruitment is below the level necessary for replacement (i.e. there is a population density below which a population will, on average, dwindle to extinction, see Larkin *et al.* 1964).

When  $\lambda_{1d} = 1$  the population is stationary and its density and structure, on average, remain constant. Variability about the stationary point is due to fluctuations in any or all of the population parameters as they respond to an altering physical environment and earlier changes in the population density or structure.

An idea of the population's behaviour in the stationary state may be obtained by simulation while allowing the parameters to vary randomly over realistic ranges. Any knowledge of the causes of fluctuations in the parameters will greatly aid this kind of investigation. For some stationary populations the fluctuations in recruitment will dominate those in the other parameters,

which may then be treated as constants. Besides simplifying analysis, the methods developed by Allen and Basasibwaki (1974) may be used to investigate the behaviour of the age class model at the stationary point.

Where  $\lambda_{1d} \neq 1$  the relationship between  $\lambda_{1d}$  and density may bear little resemblance to the growth rate of the actual population at density  $d$  since each  $\lambda_{1d}$  is defined for stability at that density. As the population progresses towards the stationary density and structure it is unlikely to remain at intervening densities long enough to attain the stable structure for those densities. The fate of unstable populations may be followed more exactly, using iterative procedures.

Solutions of  $\lambda_{1d}$  by computer take very little time for the small projection matrices usual for the age class model. However, since the size classes used in the size class model may have to be small to accommodate the population parameters accurately, the matrices involved are liable to be large. In such cases it is advantageous to work approximately, using much wider size classes. Once the general response of the population is known, the larger matrix is then used to look in detail at the specific regions of interest.

#### 1.4 MANAGEMENT OF A FISHERY

A population model may be used to predict the outcome of various possible management strategies and so allow selection of the one thought to be most desirable.



Parameters of the fishery which aid in this selection include equilibrium total catch, catch composition, catch per unit effort, population density, population structure, and the variability in each of these terms. The model may also be used to find the path which these parameters follow during the transition from the old to any new set of fishing regulations.

#### 1.4.1 Inclusion of management policies in matrix models

Management regulations usually involve one or more of the following:

- i) a limit on fishing effort
- ii) a minimum legal size of capture
- iii) closed seasons
- iv) a limit on total catch
- v) closed areas

The fishing effort alters the magnitude of the fishing mortality terms, so the relationship between fishing effort and the resulting fishing mortality must be known if a set of regulations is to be examined in terms of fishing effort. Large seasonal changes in effort may require that the year be divided into several time intervals within which fishing effort is reasonably constant. An annual projection matrix may then be formed using equation (10).

The minimum legal size of capture is the first class with a non-zero fishing mortality if the fishing selection may be considered 'knife edge'. Otherwise any suitable selection function may be used to relate size or age and fishing mortality, since fishing mortality is defined

separately for each class.

Closed seasons are an extreme example of a seasonally dependent fishing mortality, and so the relevant matrix or matrices in equation (10) would contain fishing mortality terms equal to zero.

The catch quota for a particular fishing regime may be determined directly from the equilibrium yield vector and equilibrium population density. In fixing the total catch, it must be remembered that more than one fishing strategy may result in the same equilibrium catch, and that some of these alternatives may well be undesirable. This should become obvious during development of the relationship between the equilibrium catch, fishing mortality and minimum legal size.

Investigating the effects of closed areas on a fishery requires that each area be modelled separately, with some sort of immigration-emigration relationship between them. Such a system would probably have to be investigated iteratively since migration levels may be only partially related to the local population. Immigration-emigration matrices are discussed by Pollard (1966).

#### 1.4.2 Evaluation of management strategies

If sufficient information on the species in question is available, a projection matrix (incorporating a fishing policy) may be constructed for any population density and solved for its dominant eigenvalue. The density at which the eigenvalue equals one is the equilibrium population density which would result

from the fishing regime. Multiplying the associated eigenvector by the equilibrium population density gives the equilibrium population structure. Multiplying this by a yield matrix gives the catch and its class composition. Using the relationship between fishing mortality and effort the catch per unit of effort may also then be found.

A measure of the variability to be expected from the fishery at equilibrium is obtained by iteratively following the course of the equilibrium population vector while the population parameters are allowed to vary realistically. Values for the population structure and yield during transition from one equilibrium to another may also be determined using the iterative equations. This will produce an estimate of the time taken to reach the new equilibrium.

Analysis of this type is very demanding of biological data. The density dependence of the population parameters in particular is difficult to quantify for any population. The most readily obtainable information is usually growth and mortality rates at the current population density. This may be used to form a matrix from which the equilibrium yield per recruit is calculated. At equilibrium and with constant recruitment, growth and natural mortality, the yield from the total population in any one year equals the sum of the yields taken in successive years from the initial recruitment. This may be estimated by repeatedly multiplying an initial population vector of any given number of recruits by a projection matrix, in which the fecundity terms are zero, until the number left in the vector is zero

or negligible. The sum of the yields obtained during this process is the annual yield per initial number of recruits. While this method does not predict the actual magnitude of the yield to the fishery, the relative effects of various fishing regimes may be evaluated.

Using a variety of methods, then, the catch and population characteristics resulting from exploitation may be determined. The decision as to the most desirable set of fishing regulations must then be made on the basis of the biological information and the particular social, economic and political climate of the fishery.

## 1.5 DISCUSSION

Most recent structured population models consist of equations relating the numbers in various age classes at one point in time to those present at some later time (Southward, 1968; Walters, 1969; Jones and Hall, 1972). Such equations may be conveniently expressed in matrix form. This allows a reasonably direct solution of the stable and stationary structures of the population under various fishing regimes, but does not limit the equations in their iterative applications. A population in a varying environment can only be stationary on average, and simulation of the population in the vicinity of this average is of great importance.

It will usually be obvious whether the age or size class model is most appropriate. The age class model requires far less computation and avoids the necessity of

a detailed knowledge of the growth process. However, the size class model may be usefully applied when the population parameters of a species are related more precisely to size than to age, or when there is no known method of ageing the species.

It is doubtful whether the extensive biological data required for application of the density dependent aspects of the model could be provided for a 'wild' fishery, although in most cases sufficient data could be gathered to allow analysis of the yield per recruit.

## 2. THE STUDY AREA AND POPULATION

### 2.1 THE STUDY AREA

In view of the general aims of this research, selection of a suitable study area was critical. An unfished study area was sought because working with an exploited stock

- i) introduces the possibility of human interference with tagged animals,
- ii) necessitates the separation of natural and fishing mortality, and
- iii) complicates the interpretation of the population size structures (particularly in view of the rapid changes in fishing mortality during the past 10-15 years, which would have accompanied development of the fishery).

Kaikoura was an unsuitable study area, despite the availability of data on feeding, movement, growth and reproduction of *H. iris* there (Poore, 1972a, b, c, d). Since Poore's work, fishing activities along the Kaikoura coast have greatly reduced the abundance and modified the size structure and spatial distribution of the population.

The area selected to study was Peraki Bay, on the southern coast of Banks Peninsula (Fig. 2.1), about 90 kilometres by road from Christchurch. Peraki Bay is a long, narrow indentation open to the sea to the south-west and with about 4.5 km of rocky coastline (Fig. 2.2).

Figure 2.1 Location of the Peraki Bay study area on the South Island of New Zealand. The location of place names mentioned in the text are also shown.

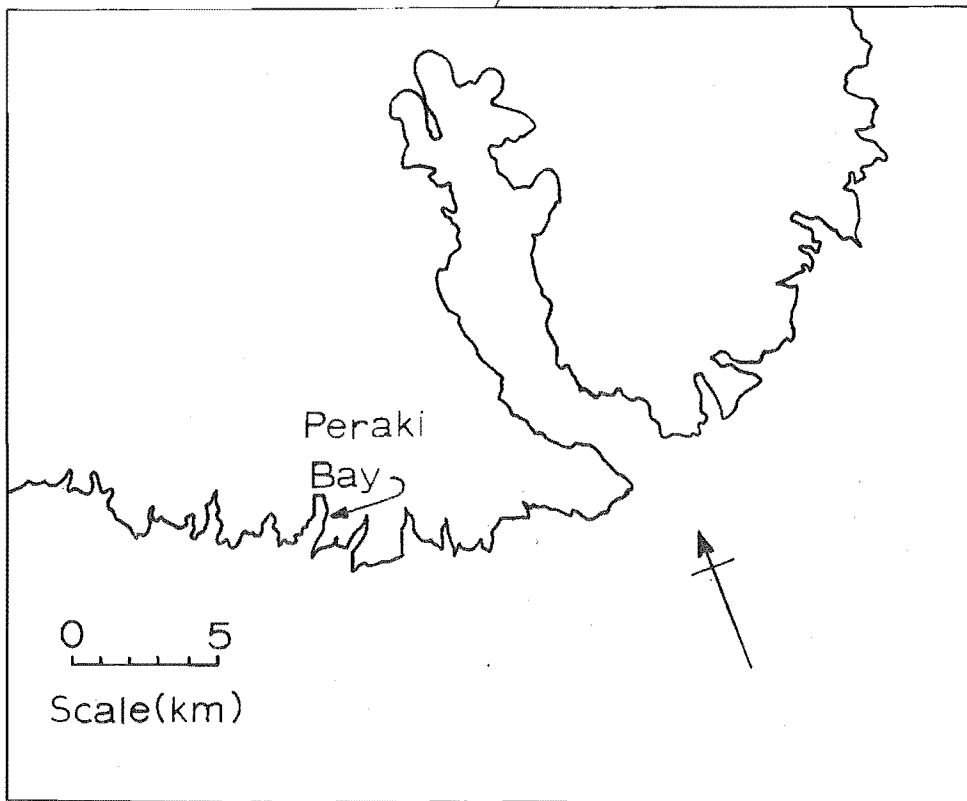
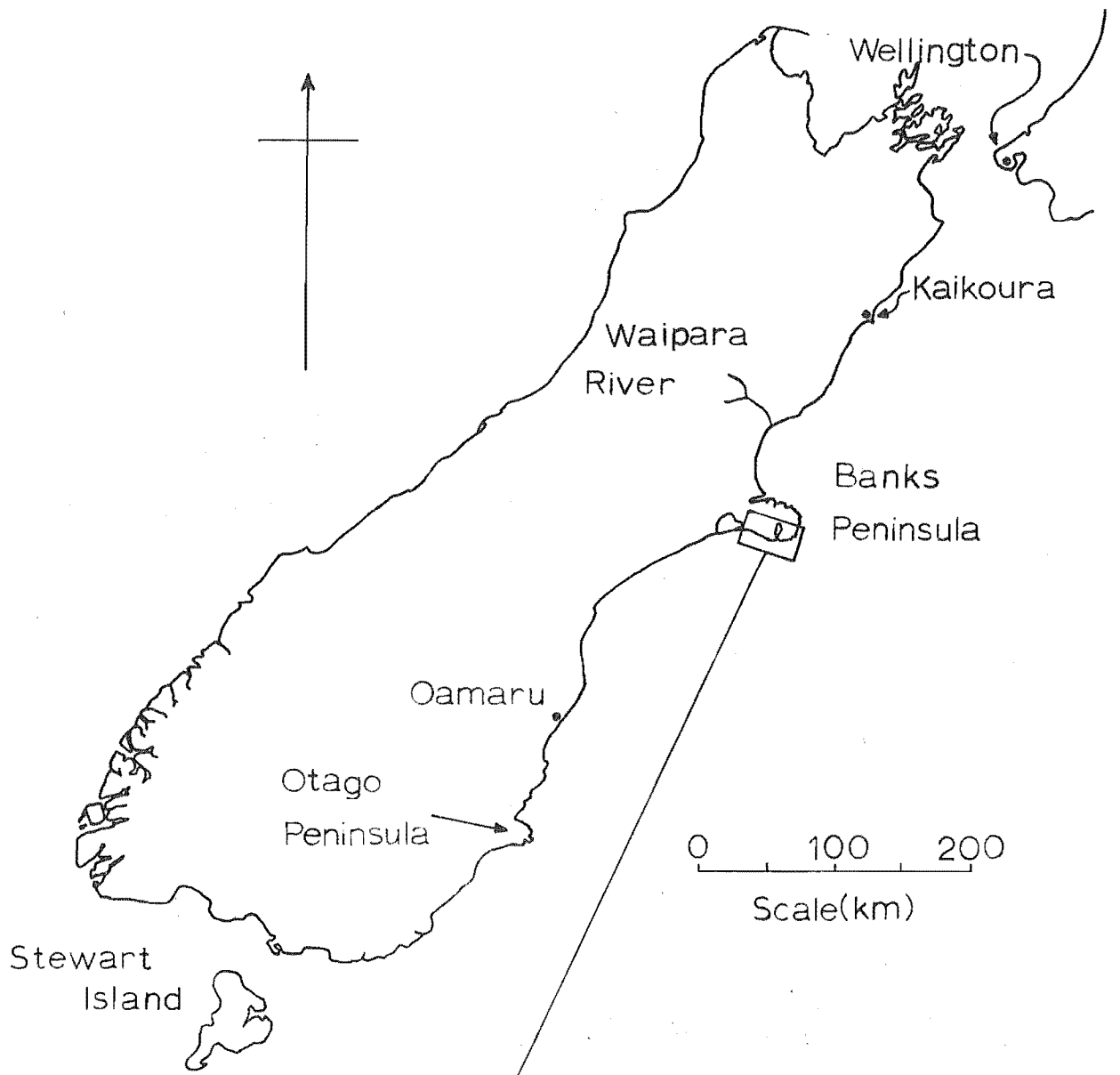
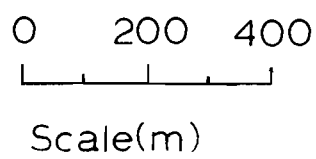
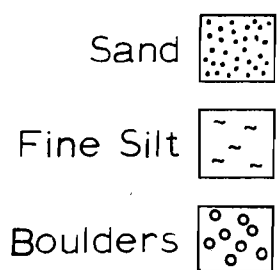
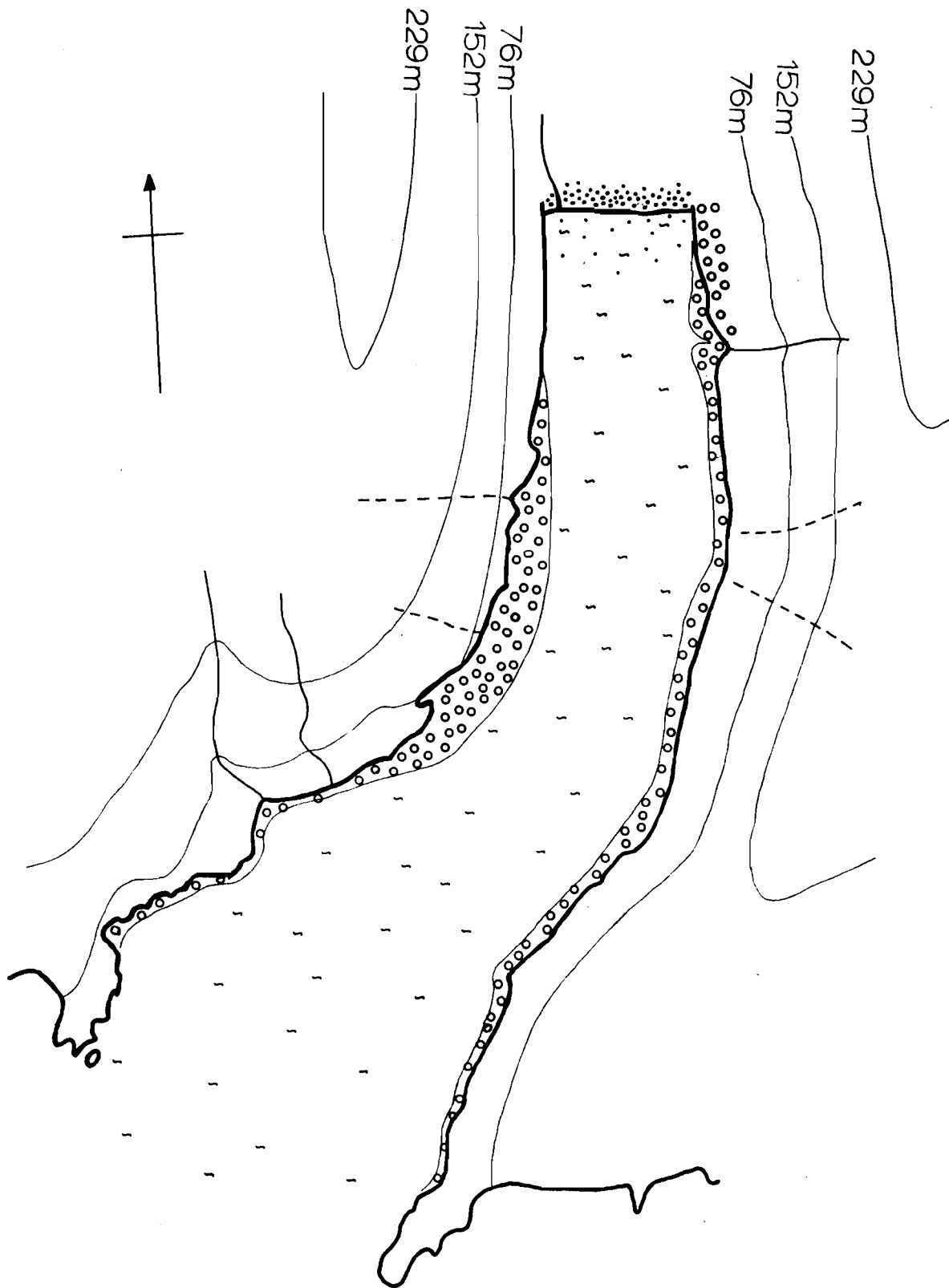




Figure 2.2 Topography and substrates of Peraki Bay.



The inner shore of the bay is a gently sloping sandy beach, grading subtidally to fine silt which forms much of the sea floor of the bay and surrounding coastal shelf. With the exception of the boulder beach in the north-eastern corner, the coastline along both sides of the bay consists of steep rockfaces extending into the sea to a depth of 3-10 m. In some areas the cliff is broken by a ledge, about 5 m wide, just above the level of high spring tides. Below the cliff the sea bottom, which consists of boulders (mostly less than about 60 cm diameter) over bedrock, shelves gently to a depth of 6-15 m. This boulder strip is from 1 to 110 m wide (Fig. 2.2) and beyond it the silt substrate extends uninterrupted to the opposite side of the bay.

Bull kelp, *Durvillea antarctica*, is found intertidally all along the eastern shore, and on the outer third of the western shore. Subtidally, the boulders adjacent to the cliff support dense beds of *Cystophora* spp., *Carpophyllum maschalocarpum*, *Glossophora kunthii* and other brown algae, while beyond this is a broad, dense forest of *Macrocystis pyrifera*. In some areas large plants of *Sargassum sinclairii* are found just above the interface between the boulder and silt substrates. Red algae are uncommon at Peraki Bay, as elsewhere on Banks Peninsula.

*Haliotis iris* are restricted to the hard substrate of the cliff and boulders, and form a continuous bed along both sides of the bay. Adults (larger than about 70 mm) occur throughout the subtidal habitat available to them, and juveniles (less than about 70 mm) are usually found beneath boulders at depths of 2-5 m. Juveniles at Peraki Bay are

not found in the sublittoral fringe, as they are in most other areas of New Zealand (Poore, 1972c; Morton and Miller, 1968), even though the boulder beach in the north-eastern corner of Peraki Bay appears to be a suitable habitat for them.

On Banks Peninsula the maximum size of *H. iris* is smaller than in most other areas of New Zealand. Few animals reach the legal minimum size for the fishery, and this, combined with poor visibility for diving, has retarded the development of a local commercial abalone fishery. These factors have not prevented pressure on accessible populations from sports divers, but the fauna of Peraki Bay has been spared the extensive human modification found in some bays on the Peninsula. Beach access by land to Peraki Bay is possible only across the property of the local farmer, Mr Bill Hall, who, along with the manager, Mr Colin Gray, has protected the bay from most forms of exploitation.

## 2.2 POPULATION SIZE AND STRUCTURE

### 2.2.1 Introduction

A population is the total number of individuals of a species occupying a defined space at a certain time. Since both the horizontal and vertical distribution of *H. iris* are size specific, it is important that the spatial aspect of the population be defined to include representative numbers of all size classes. Thus the study population was considered to occupy the whole of Peraki Bay.

The length frequency distributions of haliotids within parts of their habitat range have been established for several species (Leighton and Boolootian, 1963; Poore, 1972c; Shepherd, 1973a; Witherspoon, 1975; Newman, 1968; Forster, 1962). Usually this has been done to obtain growth rate data. However, in none of these studies was the relationship between the sampled portion and the total population known. The main reasons for this are that haliotids are usually concentrated in beds of variable size and density, and that often a significant proportion of the population is in narrow crevices or under large boulders where the animals cannot be sampled adequately (Cox, 1962). This is also true of most *H. iris* populations. But at Peraki Bay, and most of the other bays on Banks Peninsula, the animals are distributed relatively uniformly on a coastal strip of small boulders from which they can be sampled more reliably than is the case elsewhere. The number and size composition were determined for the whole study population on one occasion, and for a part of the population on two other occasions.

#### 2.2.2 Methods

An attempt to sample the Peraki Bay population by random placement of a 1 m<sup>2</sup> quadrat was found to be very inefficient in that a large proportion of the diving time was spent locating sampling points. This method was abandoned since the amount of available diving time was severely limited by unsuitable weather and low water clarity, making it important to fully utilise any sampling

opportunity. Ultimately a transect sampling method was adopted, in which the sampling unit was a one metre wide strip of sea bed, perpendicular to the coastline and extending out into the bay as far as abalone habitat occurred. Problems of over-representation (resulting from convergent transect lines) and under-representation (resulting from divergent transect lines) of parts of the sea bed adjacent to irregularities in the coastline were not encountered because the bay has essentially straight sides and the zone inhabited by *H. iris* is narrow.

The equipment used consisted of about 100 m of light line which passed through a hole half-way along a one-metre-long strip of aluminium rod. The line was weighted at one end and unwound from a weighted, lockable reel. At a sampling position on the coastline a SCUBA diver swam out from the shore, descended directly to the bottom and secured the weight at the outer edge of suitable abalone substrate. The diver then laid the line back into the shallows, locked the reel and worked back toward the outer weight, searching the metre wide strip of substrate delineated by the aluminium rod. The usual dive plan employed two divers, one (myself) to search the sea bottom and collect any abalones found, while a second put the animals into a bag and checked that none was overlooked. Searching was very slow and often involved moving large numbers of boulders to expose concealed animals (in some areas 4-5 layers of boulders lay over bedrock). Animals were measured underwater during the 1973-74 summer, but in the following years they were collected and measured later to make the best use

of diving opportunities. In both cases maximum shell length was measured to the nearest millimetre.

It was apparent from early observations that the density and size composition of the stock were not the same in all parts of Peraki Bay, so a stratified, random sampling scheme was adopted (see Snedecor and Cochran, 1967). This kind of sampling has the advantage that the variance of an estimate depends only upon the variances within the strata, and not on the variation between them. Peraki Bay was divided into six strata: 'juvenile', intermediate' and 'adult' areas on both eastern and western sides of the bay (Fig. 2.3). Sampling positions were selected randomly within strata.

Six transects were examined from the eastern intermediate (EI) stratum in January and February 1974, nineteen transects were examined during January and February 1976 (at the positions indicated in Fig. 2.3) and four transects were examined from the EI stratum in December 1976. Sampling dates were primarily determined by diving conditions. In an attempt to increase the reliability of the estimates of the numbers of juveniles present, special juvenile-only transect samples were taken during February 1974 and 1976 in which only animals smaller than 70 mm were collected. A juvenile-only sample could be completed in about half the time required for a full transect sample.

The size composition and number of animals present in each stratum were estimated from the transect data using the method outlined by Seber (1968).

Figure 2.3 The position of the sampling strata.

E.A. = Eastern Adult; E.I. = Eastern Intermediate;

E.J. = Eastern Juvenile; W.A. = Western Adult;

W.I. = Western Intermediate; W.J. = Western Juvenile.

The length of coastline encompassed by each stratum is given in brackets. Transect positions for the February 1976 sampling programme are marked +.

The position of the grid within which animals were tagged is marked X.



0 200 400



Scale(m)



W.J.

(510m)

W.I.

(560m)

W.A.

(1300m)

E.J.

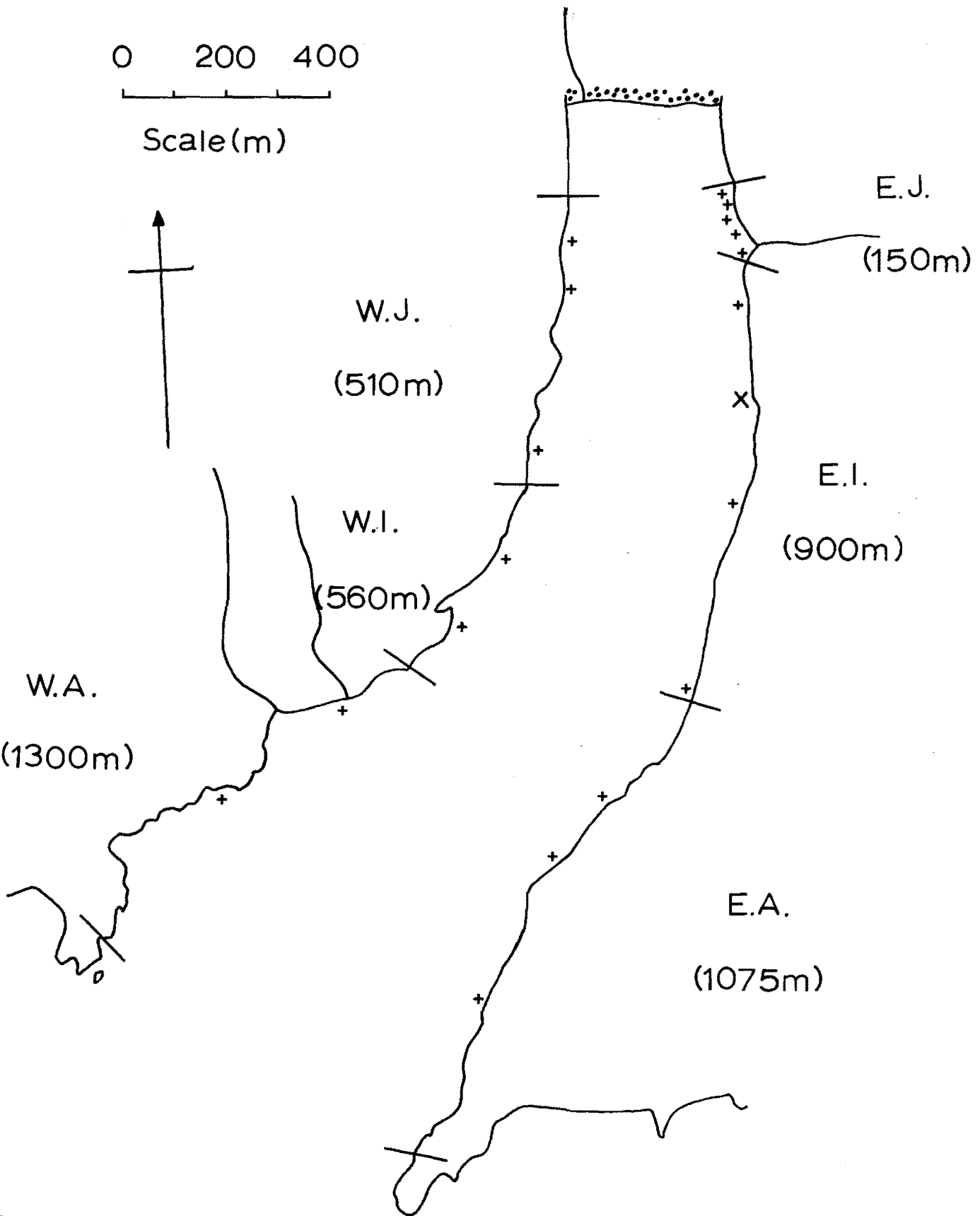
(150m)

E.I.

(900m)

E.A.

(1075m)



If  $N_{i,j}$  animals are collected in the  $i$ th sample from the  $j$ th stratum ( $i = 1, M_j$ ) and a maximum of  $T_j$  samples could be positioned in the  $j$ th stratum, then the estimated number of animals in that stratum is

$$N_j = \frac{T_j \sum_{i=1}^{i=M_j} N_{i,j}}{M_j}$$

and the variance of  $N_j$  is

$$\hat{S}_{N_j}^2 = \frac{T_j^2 V_j}{M_j} \left(1 - \frac{M_j}{T_j}\right)$$

where

$$V_j = \frac{\sum_{i=1}^{i=M_j} (N_{i,j} - \bar{N}_j)^2}{M_j - 1}$$

The population mean and variance are obtained by summing those of the individual strata.

### 2.2.3 Results

The data obtained by transect sampling are provided in Appendix 2.1. The estimates of the total population and its size structure are listed in Tables 2.1, 2.2 and 2.3 and presented graphically in Figs 2.4, 2.5 and 2.6.

The estimated population of Peraki Bay in February 1976 was 179 693 (95% confidence interval 136 548 to 222 837) and was not evenly distributed among the strata. The eastern and western shores are similar in length (2350 m and 2145 m respectively), but 71% of the abalones were found on the eastern shore.

Table 2.1 Estimated population structure for the eastern intermediate stratum in February 1974 based on the data presented in Appendix 2.1.

$N_j$  = mean number of animals in the stratum and  $\hat{S}_{N_j}$  is its standard deviation.

Size limits (mm)	$N_j$	$\hat{S}_{N_j}$
0 - 10	0	0
11 - 20	150	149
21 - 30	600	300
31 - 40	1350	384
41 - 50	1800	982
51 - 60	2100	2049
61 - 70	2100	597
71 - 80	3900	1000
81 - 90	3150	601
91 - 100	6300	1778
101 - 110	11549	1964
111 - 120	13500	2440
121 - 130	2700	802
131 - 140	0	0
Total	49199	4558

Table 2.2 Estimated population structure by strata based on February 1976 transect samples presented in Appendix 2.1  
The positions of the strata are given in Fig. 2.3.

Size limits (mm)	EJ		EI		EA		WJ		WI		WA		TOTAL	
	N <sub>j</sub>	$\hat{S}_{N_j}$	N <sub>j</sub>	$\hat{S}_{N_j}$	$\hat{N}$	$\hat{S}_{N_j}$	N <sub>j</sub>	$\hat{S}_{N_j}$	N <sub>j</sub>	$\hat{S}_{N_j}$	$\hat{N}$	$\hat{S}_{N_j}$	N <sub>j</sub>	$\hat{S}_{N_j}$
0 - 10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 - 20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21 - 30	45	22	300	299	0	0	0	0	0	0	0	0	345	300
31 - 40	105	43	900	898	0	0	400	169	0	0	0	0	1345	912
41 - 50	240	81	0	0	0	0	170	169	0	0	0	0	410	192
51 - 60	360	71	600	598	0	0	340	339	0	0	0	0	1300	611
61 - 70	300	72	1200	792	866	432	340	169	186	186	0	0	2894	940
71 - 80	870	126	1200	598	1300	749	510	0	933	372	0	0	4813	1037
81 - 90	540	36	2700	898	5633	5626	1189	339	746	186	0	0	10809	5711
91 - 100	780	225	8100	2261	13000	9975	510	293	1493	493	0	0	23883	10051
101 - 110	1140	151	14700	1963	22533	9974	4080	1058	5040	1706	1071	1073	48568	10227
111 - 120	675	224	13200	792	25566	6376	3060	587	4293	671	6451	2148	53245	6836
121 - 130	60	36	2400	1079	6500	5193	680	448	1120	558	14512	2684	15272	5989
131 - 140	0	0	0	0	1733	1145	0	0	186	186	4837	2684	6757	2925
Total	5115		45300		77131		11279		13997		26871		179693	18243
No./metre coastline	34.1		50.3		59.3		22.1		24.9		24.9			

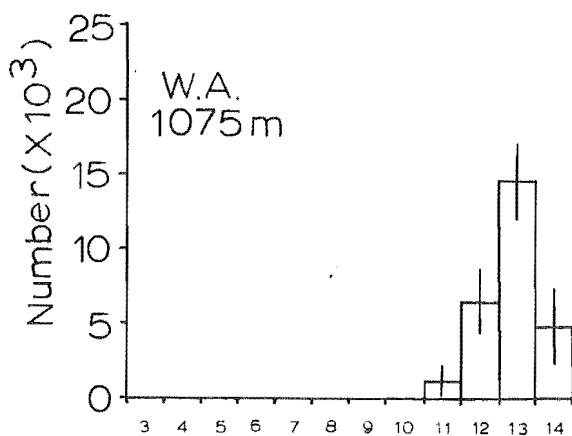
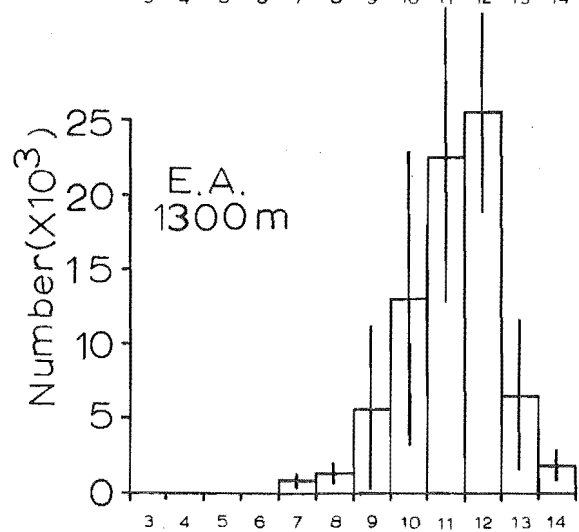
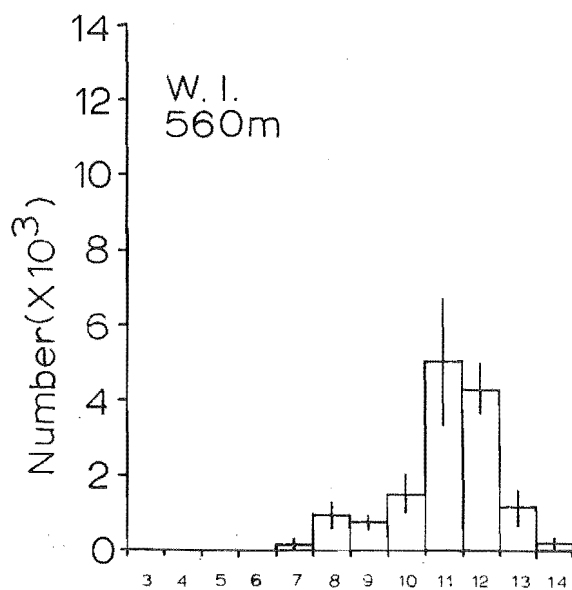
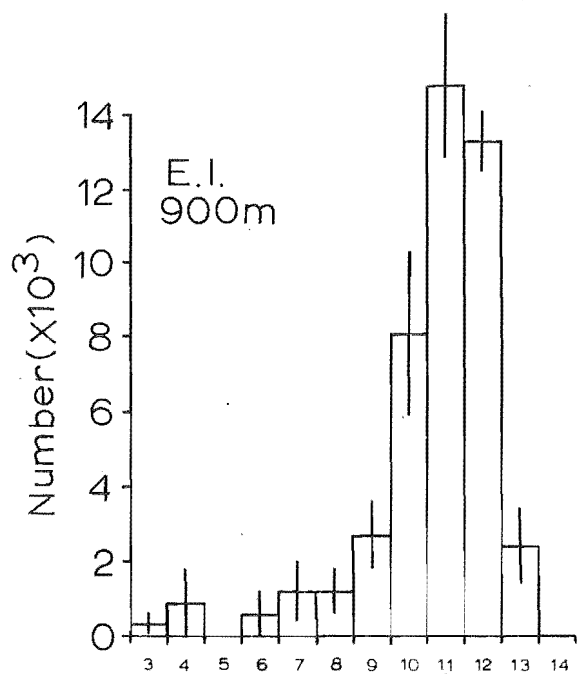
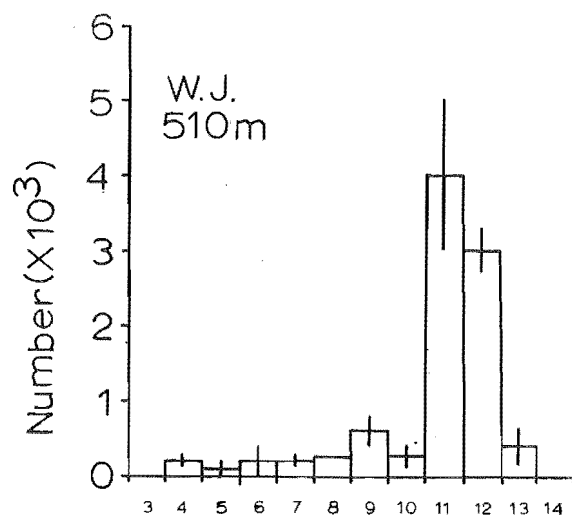
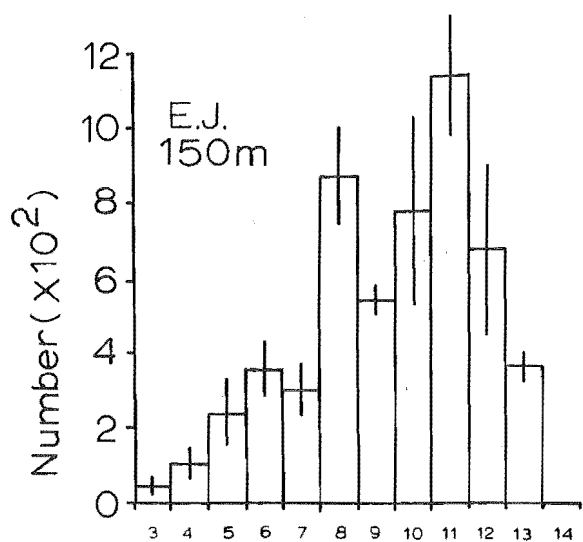
Table 2.3 Population structure of the eastern intermediate stratum in December 1976, based on the data presented in Appendix 2.1

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Size limits (mm)	$N_j$	$\hat{S}_{N_j}$
0 - 10	0	0
11 - 20	0	0
21 - 30	0	0
31 - 40	0	0
41 - 50	450	259
51 - 60	225	225
61 - 70	675	429
71 - 80	675	224
81 - 90	2025	564
91 - 100	8100	1680
101 - 110	16425	4137
111 - 120	11925	2086
121 - 130	2700	970
131 - 140	225	225
Total	43425	4839

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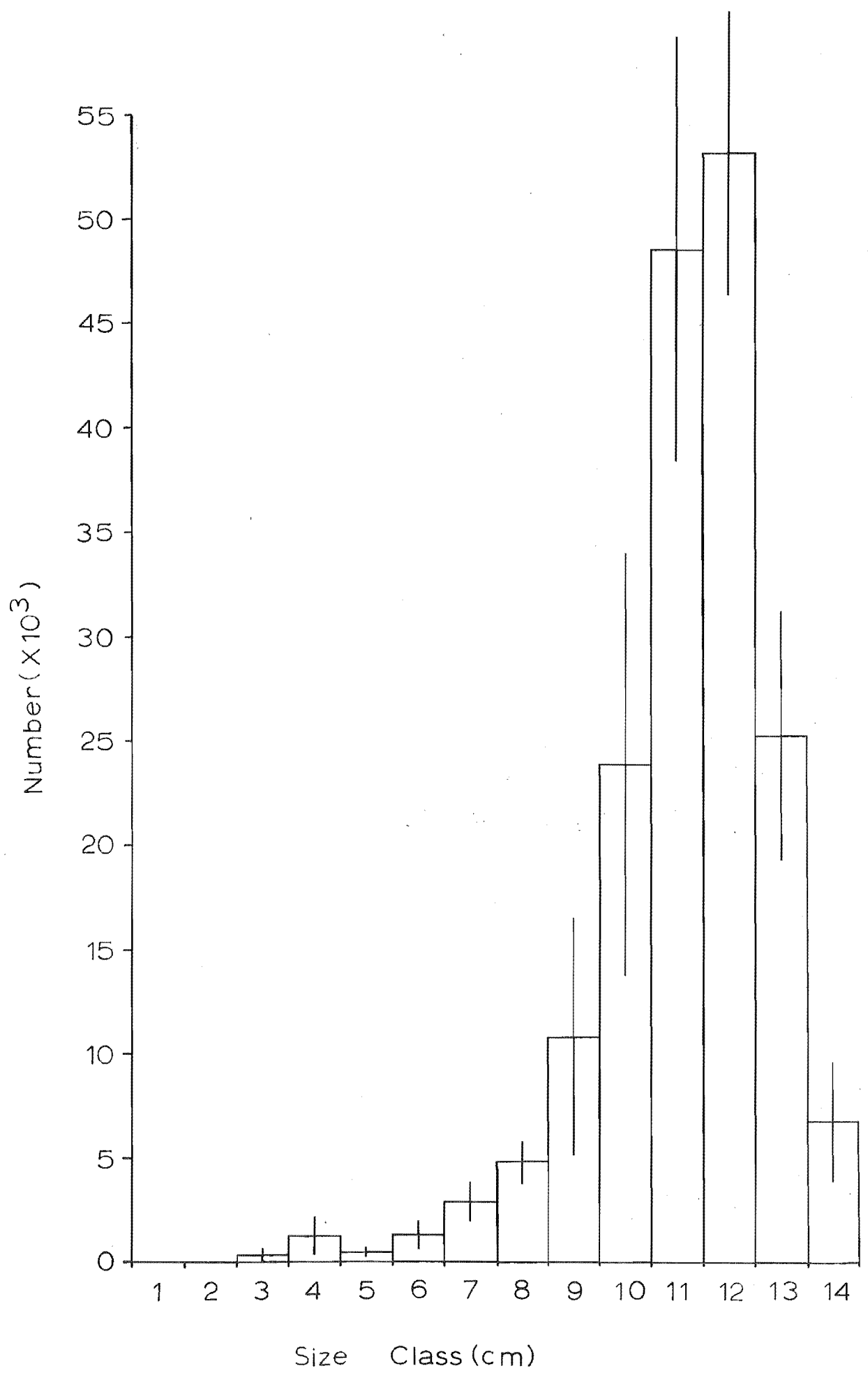
Figure 2.4 Population size structure by stratum in  
February 1976. Bars indicate  $\pm$  one standard deviation.  
Based on Table 2.2. Each size class,  $i$ , includes  
animals from  $(i - 0.9)$ cm to  $i$  cm.



Size : Class( c m)

Figure 2.5 Size structure of total population at Peraki Bay in February 1976. Bars indicate  $\pm$  one standard deviation. Based on Table 2.2. Each size class,  $i$ , includes animals from  $(i - 0.9)$  cm to  $i$  cm.





There were also more juveniles on the eastern than on the western side. The number of abalones per metre of coastline was similar in all strata on the western coast, but on the eastern coast it increased with increasing distance from the inner beach (Table 2.2). This result is contrary to that expected from consideration of differences in the width of suitable substrate on the two sides of the bay (Fig. 2.2). On the eastern shore the substrate is uniformly narrow, whereas on the western shore the substrate width varies.

The average length of abalones increases with increasing wave exposure if each side of the bay is considered separately, but the trend becomes confused when the bay is considered as a whole. The relative exposures of the strata are  $WJ < WI < EJ < EI < EA < WA$ . Only about 14 400 legal size animals (8% of the population) were present in February 1976, and most of these were on the exposed headlands.

The size composition of the population is strongly skewed to the right (Fig. 2.5), suggesting that most of the population consists of old individuals and that there is a low annual recruitment of juveniles.

During the February 1976 transect sampling programme one metre per 225 metres of coastline was examined, resulting in the measurement of approximately one animal for every 260 in the population. A suboptimal allocation of effort during the February 1976 sampling programme resulted in very large variances for the estimates of the total number of animals in the 81 to 130 mm size range (Table 2.2, Fig. 2.5).

The bulk of this variability originated in the eastern adult stratum, which should have been sampled more intensively. The means and variances of the numbers in each size class present within this stratum as a proportion of the total population mean and variance are:

Size (mm)	Proportion of total population in EA stratum	Proportion of $\hat{S}^2$ total due to $\hat{S}^2$ EA
61 - 70	0.28	0.21
71 - 80	0.27	0.52
81 - 90	0.52	0.97
91 - 100	0.54	0.94
101 - 110	0.46	0.91
111 - 120	0.48	0.87
121 - 130	0.26	0.75
131 - 140	0.25	0.15

The eastern adult stratum contained about 28% of the available habitat of the bay, but supported a disproportionate number of animals in the size range 81-120 mm and contributed the bulk of the variance of the estimates relating to these size classes.

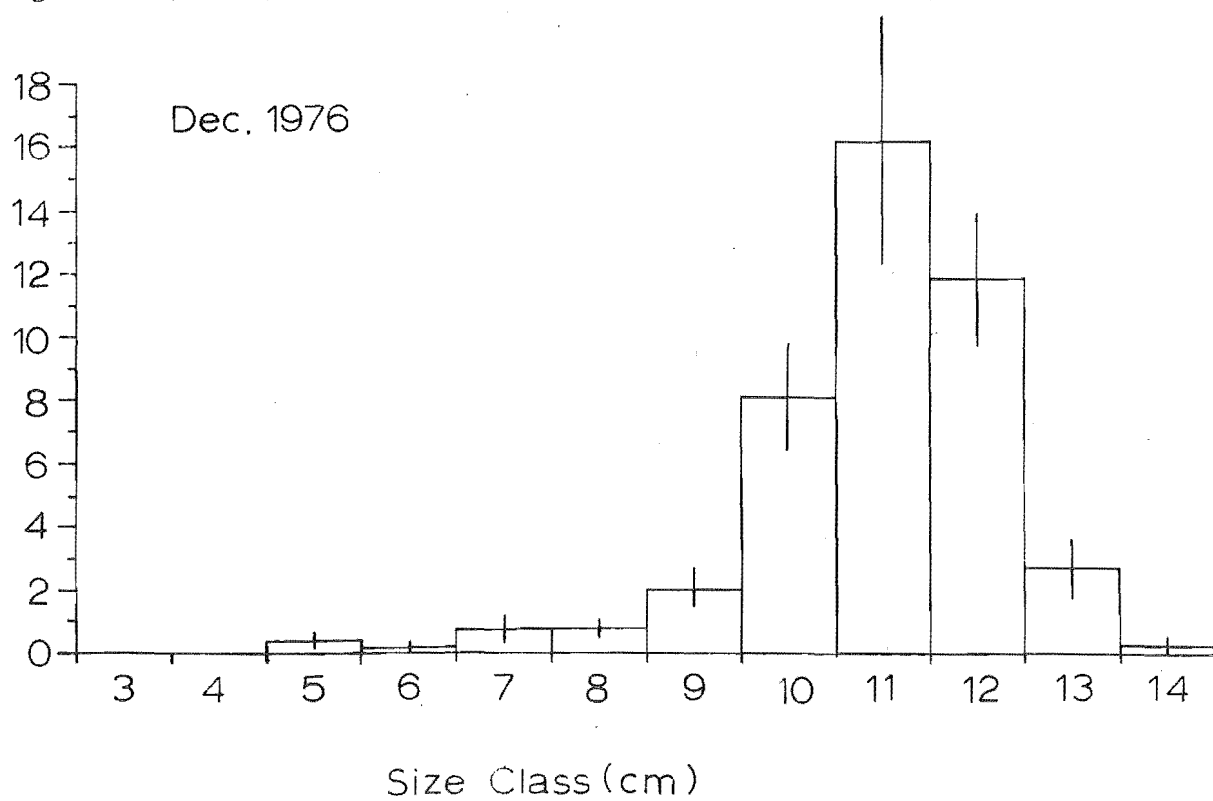
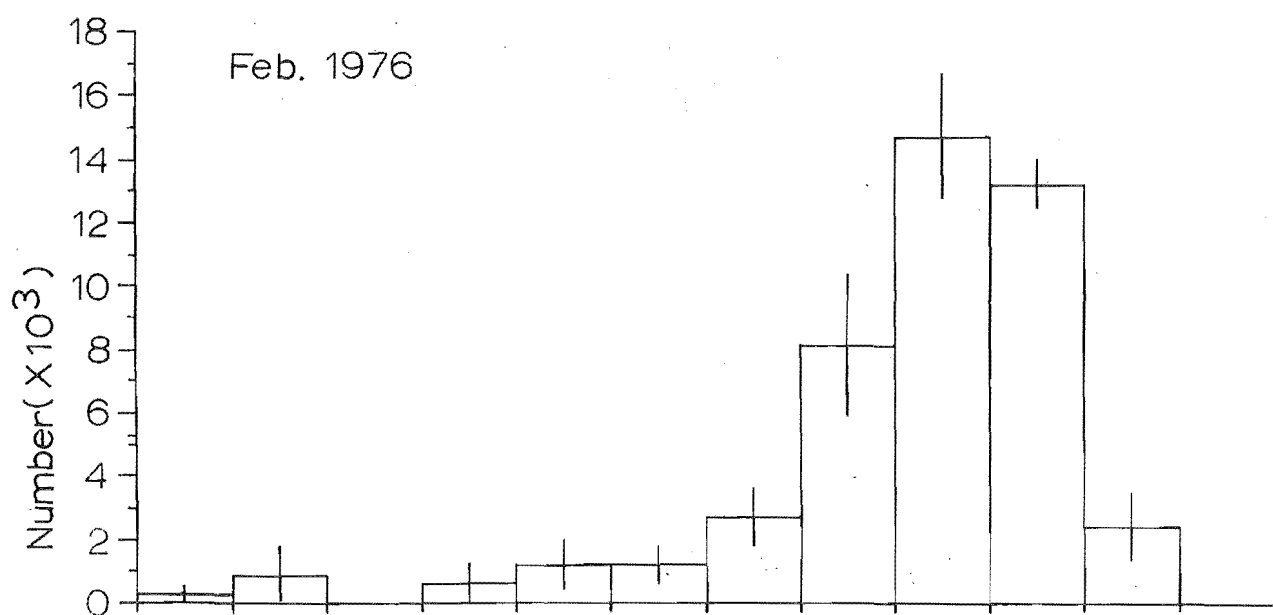
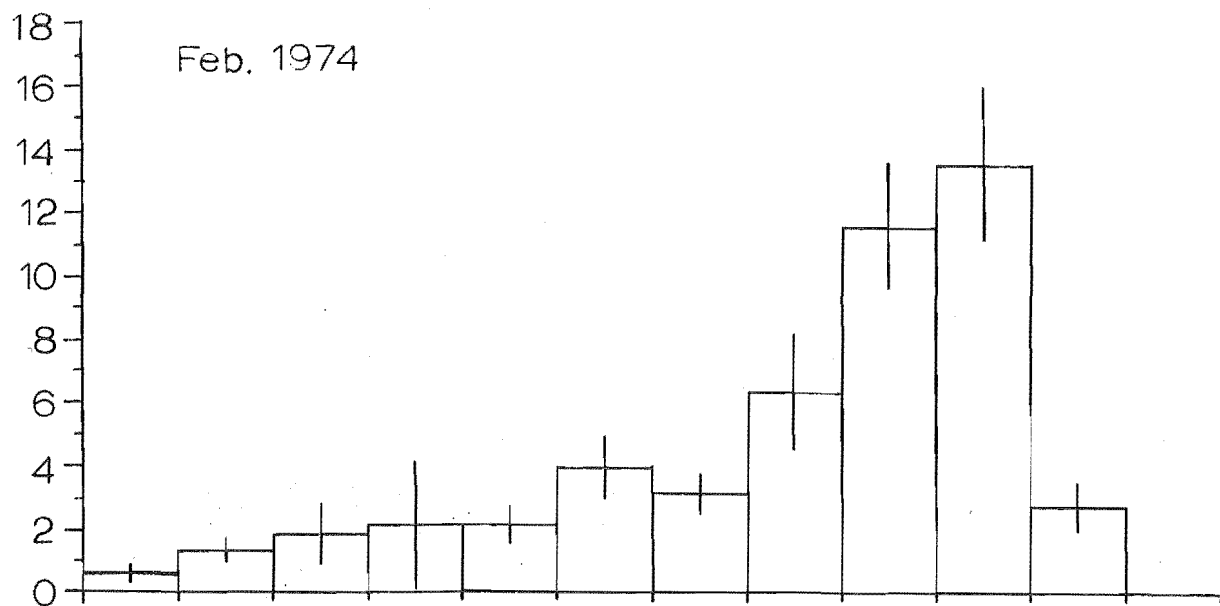
The number and size composition of abalones in the eastern intermediate stratum in February 1974, February 1976 and December 1976 are given in Fig. 2.6, and show consistent temporal changes in the size structure. In 1974 the number of animals in each size class up to the 71-80 mm size class progressively increased, indicating that the smaller size classes were not representatively sampled or/and recruitment had been decreasing for some years prior to 1974.

Figure 2.6 Size structure of *H. iris* within the Eastern Intermediate stratum on three sampling occasions.

Vertical bars indicate  $\pm$  one standard deviation.

Based on Tables 2.1, 2.2 and 2.3.

Each size class,  $i$ , includes animals from  $(i - 0.9)$  cm to  $i$  cm.



The animals in the poorly represented 20-40 mm size range in 1974 would have grown to be about 50-75 mm by February 1976 (see Chapter 3) and, as expected, the number of animals in this size range in February 1976 had decreased relative to the 1974 estimates. The number of animals in the 20-40 mm range present in February 1976 was still very low, while the number in the 91-110 mm size range had increased. By December 1976 the animals in the 20-40 mm size range in 1974 would have grown to be about 70-90 mm, and these size classes are poorly represented in the December 1976 size structure. The low number of 20-40 mm animals present in February 1976 are consistently reflected in the low number of 40-60 mm animals present in December 1976. The total number of animals in the EI stratum at the various sampling times <sup>was</sup> were:

February 1974	49	199	(S = 4558)
February 1976	45	300	(S = 3715)
December 1976	43	425	(S = 4839)

Although the differences between years are not statistically significant, they indicate that mortality may have been exceeding recruitment during the period of study.

The changes in size structure suggest that strong recruitment occurred for several years at some time prior to 1974, after which there was low recruitment which continued during the period encompassed by this study. Interpretation is complicated by the possibility of an emigration-immigration imbalance for the arbitrarily defined stratum and because animals less than 10 mm in length were not found during the transect sampling programme, despite particular care being taken to locate them.

However, the consistency of the trends suggests that these are minor sources of error.

#### 2.2.4 Discussion

The large variances associated with the estimates of population size and structure in this study highlight the problems facing haliotid research workers in areas where populations are distributed far less favourably than at Peraki Bay.

The number and spatial distribution of abalones on the eastern and western sides of Peraki Bay are strikingly different, and since movement of post-larval *H. iris* across Peraki Bay is unlikely, these differences indicate that some of the population parameters of *H. iris* vary within the bay. There were fewer abalones on the western side of Peraki Bay than on the eastern side, which could be due to a higher post-recruit (animals > 20-40 mm) mortality on the western side. There were also fewer juvenile animals on the western side than on the eastern side, perhaps indicating a difference in recruitment (of 20-40 mm animals) between the two sides which alone could cause the total number of animals to be lower on the western side. A difference in recruitment could be due to differences in the number of larvae settling and/or their subsequent, pre-recruitment survival. It is likely that the mortality on the western side of Peraki Bay is higher than on the eastern side because fine sediment accumulates more readily in the sheltered WJ and WI strata than elsewhere in the bay. Burial by sediment is probably the main cause of mortality among abalones at Peraki Bay (see Chapter 6).

### 3. GROWTH

#### 3.1 INTRODUCTION

Growth is probably the most extensively studied aspect of haliotid biology (see Crofts, 1929, and Forster, 1967, for *H. tuberculata*; Leighton and Boolootian, 1963, for *H. cracherodii*; Newman, 1968, for *H. midae*; Sasaki, 1926, for *H. gigantea*; Sakai, 1962, for *H. discus hannai*; Oba, 1964, for *H. diversicolour supertexta*; Poore, 1972c, for *H. iris*, *H. australis* and *H. virginea*; Harrison and Grant, 1971, for *H. ruber*; Cox, 1962, for *H. rufescens*). For most species, growth is adequately described over a broad size range by the Von Bertalanffy growth equation, and Poore (1972c) has compared the growth parameters of *H. iris* from Kaikoura with those previously published for the genus. Although there is considerable variation of growth rate and asymptotic length both within and between species, the parameter estimates given by Poore for *H. iris* at Kaikoura,  $K = 0.3104$  and  $L_{\infty} = 146.2$  mm, are within the range reported for the genus. However, the growth parameters of *H. iris* at Peraki Bay could be different to those of the Kaikoura population since the largest abalone recorded at Peraki Bay was 140 mm (see Chapter 2), whereas the largest recorded from Kaikoura was 177 mm (Poore, 1972c). Because the growth relationship is fundamental to the application of the population model presented in Chapter 1, its precise nature must be determined.



Growth of small abalones at Peraki Bay was determined by examination of changes in their length frequency distribution, and growth of larger animals was estimated from the results of tagging experiments.

### 3.2 METHODS

Different methods were employed to estimate the growth rates of juvenile ( $\leq 70$  mm in length) and adult (larger than 70 mm) animals.

#### Juveniles

Poore (1972c) has shown that the first two or three year classes may be separated by length frequency analysis. Samples of juvenile *H. iris* were collected from Peraki Bay on five occasions: November 1973, February 1974, May 1975, November 1975 and February 1976. The May and November samples were each collected during three ninety-minute SCUBA dives in which the substrate was searched and all juveniles encountered were collected, measured to the nearest millimetre and returned to the sea. The length frequency distributions in February 1974 and February 1976 were each based on animals collected during one such search, together with all juveniles collected at these times during the transect sampling programme (see Chapter 2). Each length frequency distribution was analysed for its constituent normal distributions by the method of Cassie (1950).

#### Adults

Regular growth rings are not present in the shell of *H. iris* (Poore, 1972c) and so the growth of adults was

investigated by measuring the growth increment of tagged individuals.

It was hoped that a closely monitored group of tagged adults would provide information on growth, movement and mortality. This required both a tagging method which did not affect the animal and an accurate method of determining the position of each tagged animal. For spatial reference it was decided to construct an underwater grid, within which the study animals would be tagged. Poore's (1972b) work suggested that *H. iris* are reasonably sedentary.

A 10×18 metre grid was constructed at a depth of 3-7 m in a typical part of Peraki Bay (Fig. 2.3). The grid consisted of an outer rectangle of 20 mm galvanised chain, weighted at each corner with a 120 kg railway wagon wheel. Cross-lines of 10 strand monel-metal wire rope were attached to the outer rectangle at 2 m intervals, so dividing the area within the grid into forty 2×2 m squares. Unfortunately the wire rope was removed by wave action within a few weeks of the grid's construction, but the chain and wheels were still intact after 15 months. (Without the internal mesh movement could not be accurately measured and so will not be discussed in detail.)

In most previous tagging experiments on haliotids (see Poore, 1972c, and Newman, 1968), the animals were collected, brought to the surface and a tag attached by a fine wire threaded through the respiratory pores. Harrison and Grant (1971) showed that such handling, and the presence of the wire loop, could adversely affect the growth of tagged animals, so methods of cementing tags on to the shell without

removing the animal from the substrate were investigated. Several adhesives were tested, of which only Expocrete U.A. (Expandite Company) set correctly under total immersion in sea water and was easily manipulated by a diver. However, over the temperature range encountered (usually  $10^{\circ}$ - $18^{\circ}$ C) about 18 hours were required before the tag was attached to the shell firmly enough to resist even moderate wave action. This restricted tagging operations to when the sea was very calm. It was not necessary to clean the shell of encrusting algae before application of the adhesive.

To test the tagging method, U-shaped monel-metal tags (Fig. 3.1a) were attached to the shells of 40 adult *H. iris* which were on the relatively sheltered boulder beach in the north-eastern corner of Peraki Bay. Tag retention for this initial group was very good (90% over 3 months) and in May 1975 sixty-five animals within the underwater grid were tagged using the same method. However, during the following two months it became apparent that the tags were too large and they caught on rock overhangs and other irregularities (uncommon on the inner shore) which tore them from the animal, usually along with a large portion of the upper layers of the shell. A small (5×10 mm) laminated plastic tag (Fig. 3.1b) was later tested within the area of the grid and found to be more suitable. Thirty animals within the grid were marked using these tags in November 1975, and a further 120 in February 1976. Remeasurements were made in March, April and December 1976 and in January 1977. Remeasurement of tagged animals during the winter of 1976 was prevented by poor diving conditions.

Figure 3.1(a) U-shaped monel-metal tag initially tested.

Figure 3.1(b) Low profile, engraved plastic tag  
finally used.



To establish the length-weight relationship of the Peraki Bay population, the foot (eviscerated body) weight and total shell length of animals were recorded.

### 3.3 RESULTS

The length-foot weight relationship is shown in Fig. 3.2. Direct least squares estimates (Conway, Glass and Wilcox, 1970) of the parameters of

$$W = aL^b$$

are  $a = 2.184 \times 10^{-5}$  and  $b = 3.1997$  where  $W$  is weight in grams and  $L$  is length in mm. The value of  $b$  is significantly different from 3.0 ( $t_s = 2.08$ , d.f. = 265). However, this function does not adequately describe the length-weight relationship for lengths less than about 80 mm, and so a polynomial was also fitted. Inclusion of terms beyond the quadratic did not significantly reduce the mean square error further ( $\alpha = 0.05$ ), and so

$$W = 26.0669 - 1.240 L + 0.01535 L^2$$

was accepted as an adequate description of the relationship (Fig. 3.2).

The length frequency distributions of juvenile *H. iris* are shown in Fig. 3.3. The mean length of each of the year classes separated by the method of Cassie (1950) is plotted against age in Fig. 3.4. Ages were assigned assuming that spawning occurred in early March each year (see Chapter 4 and Poore, 1972d) and so are not exact. The estimates provided by Cassie's graphical method were checked by reanalysing the data by the method of Young and Skillman (1975).

Figure 3.2 Length-foot weight relationship for *H. iris*  
at Peraki Bay.

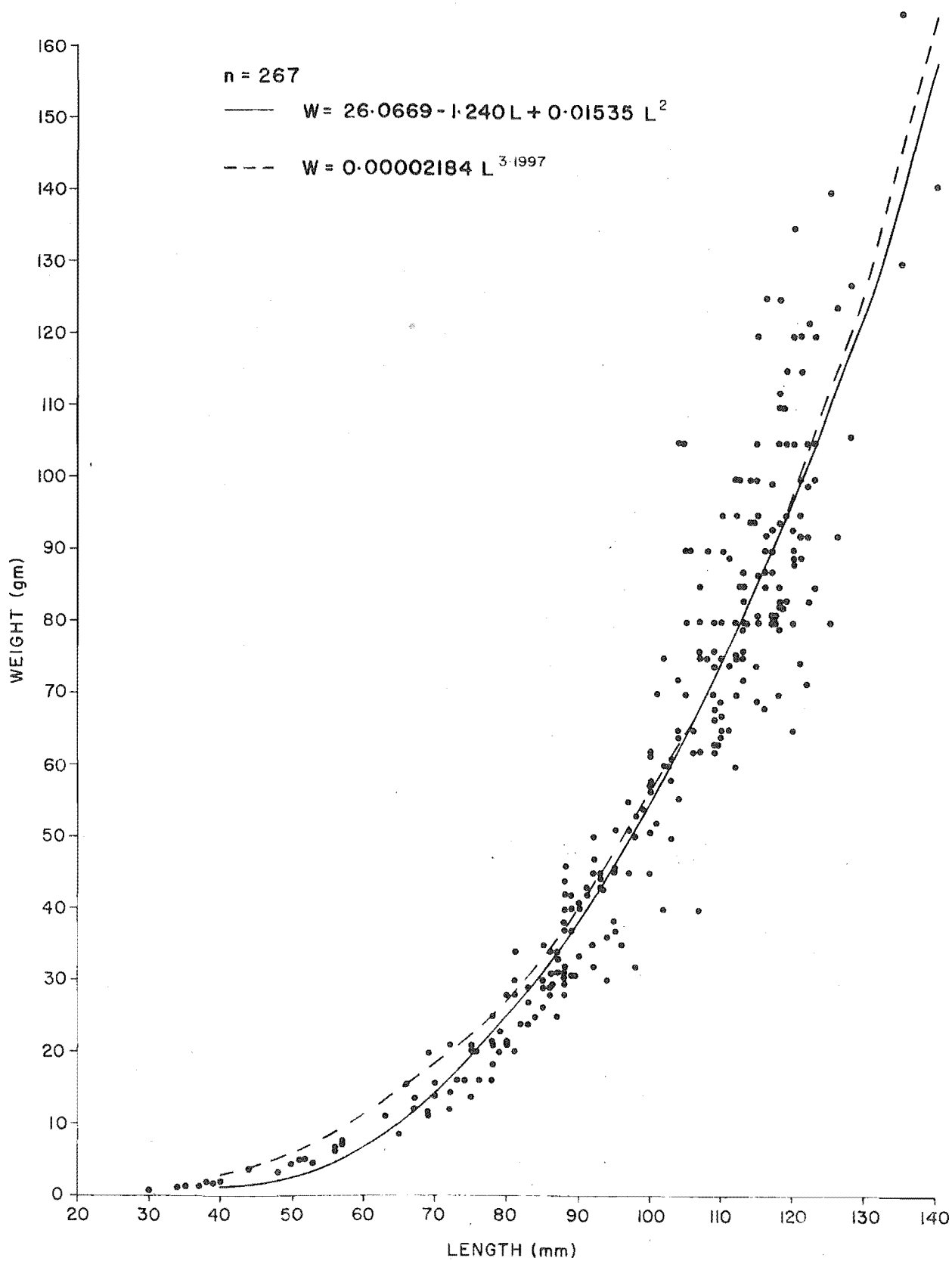
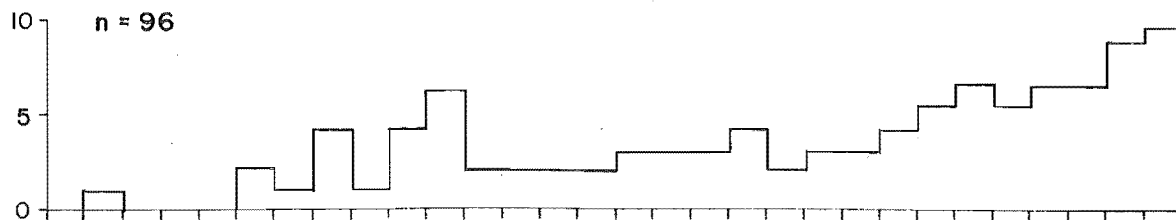




Figure 3.3 Length frequency of *H. iris* less than 70 mm  
for five sampling occasions.

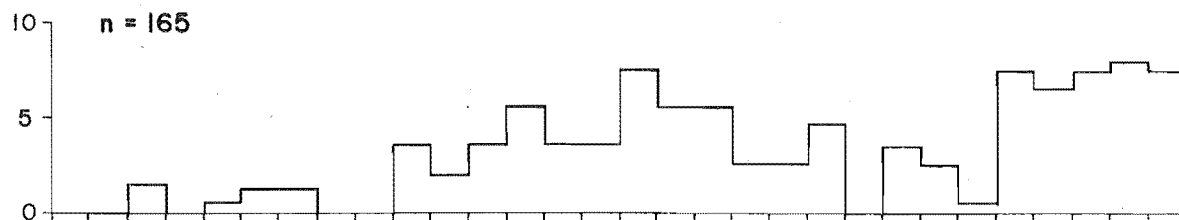
NOV. 1973

n = 96



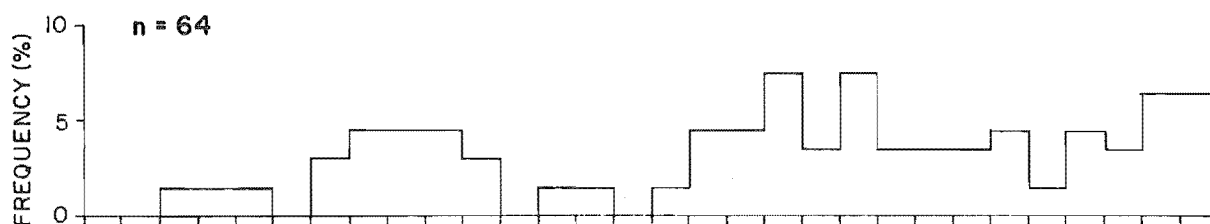
FEB. 1974

n = 165



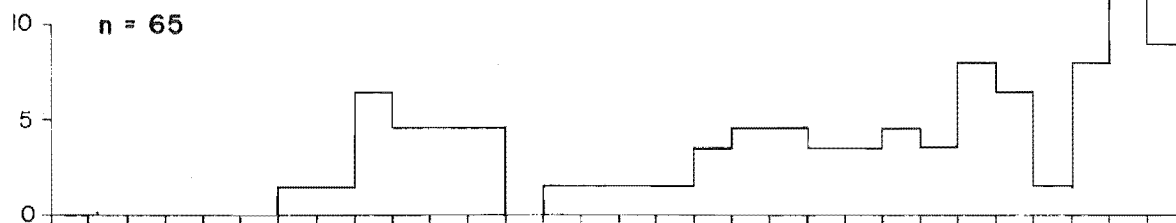
MAY 1975

n = 64



NOV. 1975

n = 65



FEB. 1976

n = 126

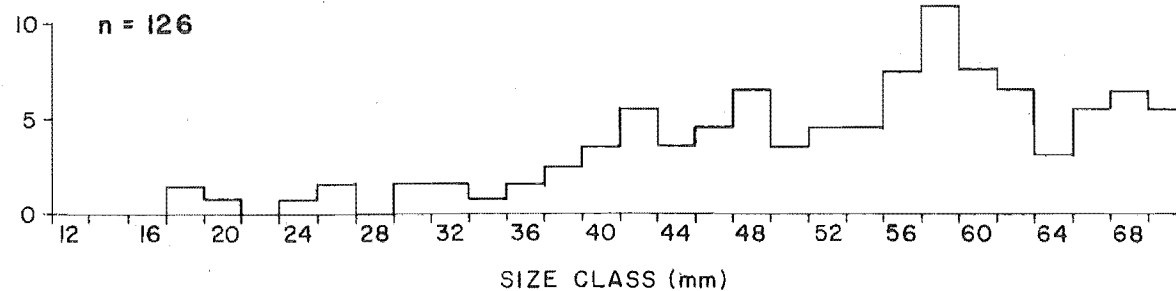


Figure 3.4 Length-age relationship for *H. iris* less than 70 mm at Peraki Bay. Each point gives the mean  $\pm$  2 standard deviations for the normal distributions separated from the length frequency histograms shown in Fig. 3.3. The number of animals from each distribution is given in brackets for each sampling occasion (numbers obtained from Table 3.1).

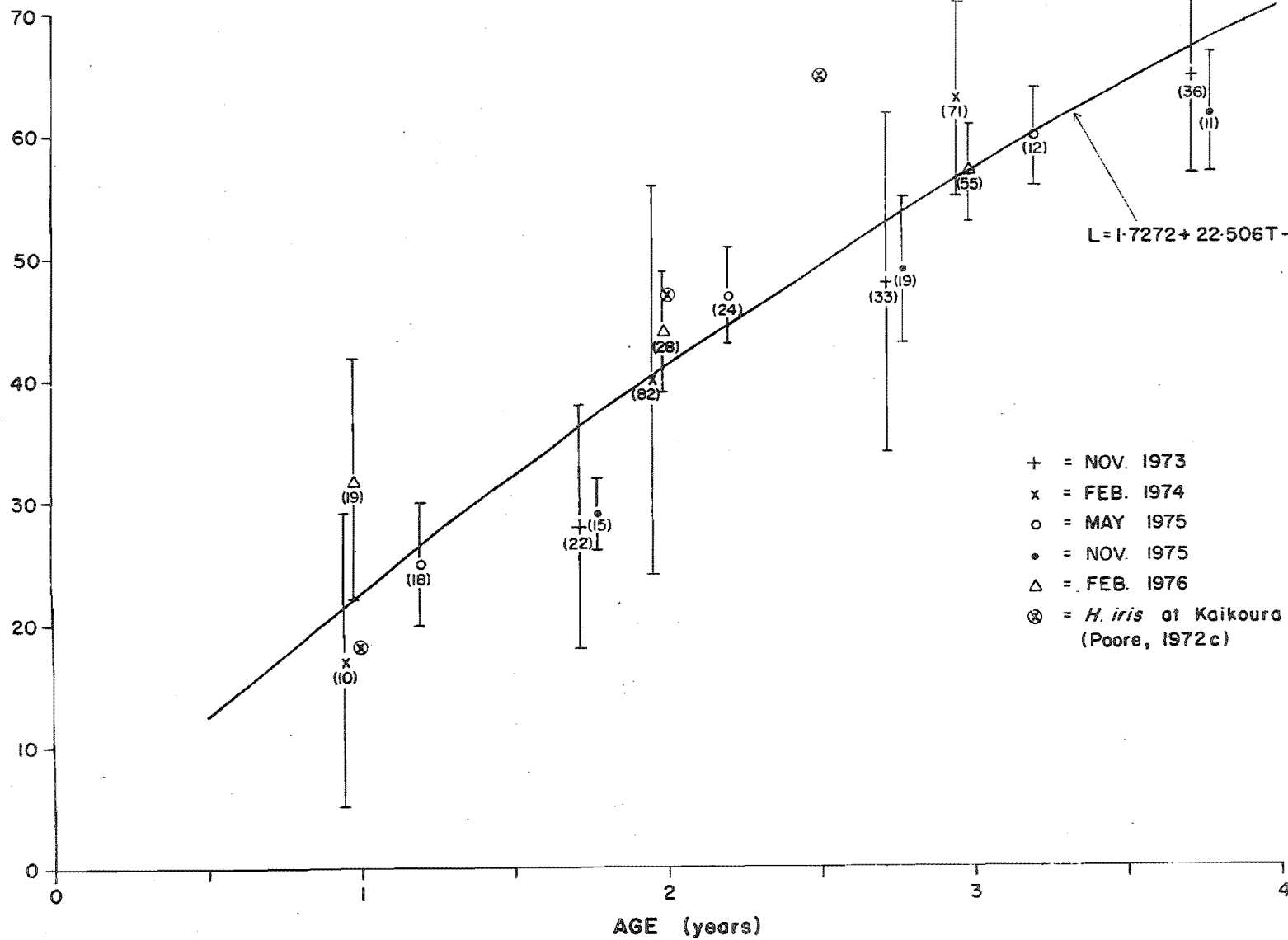
The polynomial was fitted by least squares to the means weighted by the reciprocal of  $S_Y^2$ .

The corresponding relationship for *H. iris* at Kaikoura is also shown (after Poore, 1972c).

LENGTH (mm)

$$L = 1.7272 + 22.506T - 1.2353T^2$$

- + = NOV. 1973
- x = FEB. 1974
- o = MAY 1975
- = NOV. 1975
- Δ = FEB. 1976
- ⊗ = *H. iris* at Kaikoura  
(Poore, 1972c)



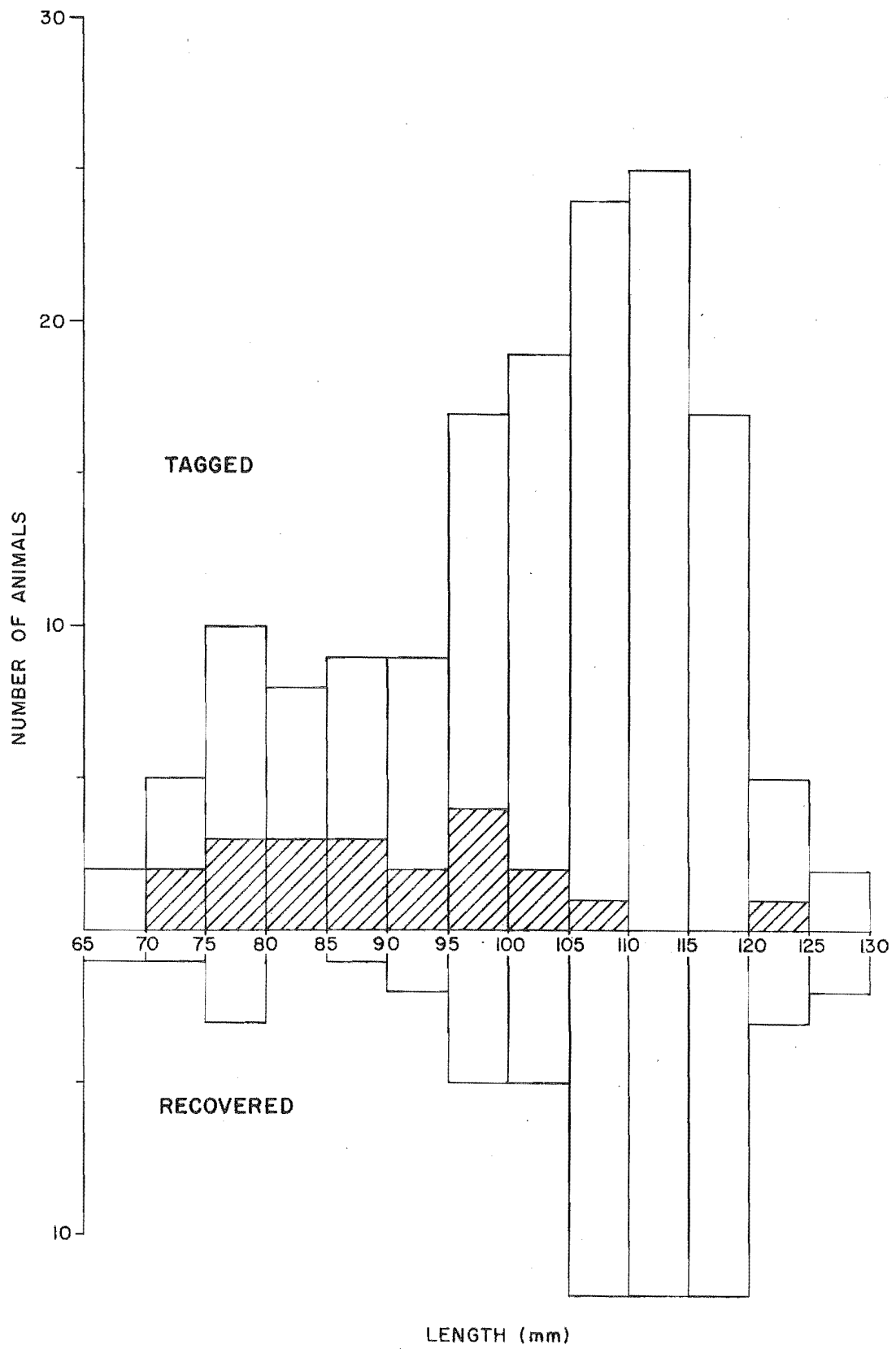
In this method several polynomials of different order are fitted to the cumulative probability data, and differentiated to provide the inflection points. Analysis then proceeds as described by Hasselblad (1966). There was generally good agreement between the results of this method and those provided by Cassie's method (Table 3.1).

Fifty-nine (39%) of the 150 abalones tagged were recovered on one or more occasions, and 23 detached tags were found. There were few multiple recaptures (fifty recaptured once and nine recaptured twice), mainly because poor diving conditions prevented observation of the tagged group during the winter of 1976. The length frequency distributions of the animals initially tagged, and of those recaptured, are shown in Fig. 3.5. The recovery rate was lower for animals less than 100 mm in length than it was for larger animals. The initial lengths of animals known to have lost their tags (Fig. 3.5) suggest that tag retention was better among large animals than small ones. This may be because the shells of large abalones are usually more corrugated than those of small animals, and so provide a better attachment surface for the adhesive. It is also possible that small animals move greater distances than large ones, so that a larger proportion of small animals left the vicinity of the tagging site. Although the sea bed was searched for about 150 m on both sides of the grid, all animals re-measured were within 50 m of their initial position.

Table 3.1 The parameters of the normal distributions separated from each juvenile length frequency distribution by the methods of Cassie (1950) and Yong and Skillman (1975)

		Cassie			Yong & Skillman		
Nov. 1973	age class	1+	2+	3+	1+	2+	3+
n = 96	mean length (mm)	28	48	65	28	42	61
	S (mm)	5	7	4	3.0	10	2
	proportion	0.23	0.35	0.38	0.12	0.60	0.26
Feb, 1974	age class	0+	1+	2+	0+	1+	2+
n = 165	mean length (mm)	17	40	63	15	42	64
	S (mm)	6	8	4	4	9	2
	proportion	0.06	0.50	0.43	0.04	0.67	0.29
May 1975	age class	1+	2+	3+	1+	2+	3+
n = 64	mean length (mm)	25	47	60	27	48	60
	S (mm)	5	4	4	5	4	2
	proportion	0.28	0.375	0.187	0.34	0.47	0.18
Nov. 1975	age class	1+	2+	3+	1+	2+	3+
n = 65	mean length (mm)	29	49	62	30	50	61
	S (mm)	3	6	5	3	6	3
	proportion	0.23	0.29	0.17	0.31	0.42	0.26
Feb. 1976	age class	0+	1+	2+	0+	1+	2+
n = 126	mean length (mm)	32	44	57	31	42	58
	S (mm)	10	5	4	5	3	3
	proportion	0.15	0.22	0.44	0.09	0.18	0.69

Figure 3.5 Length frequency of animals tagged (above) and subsequently recovered (below). The length frequency of animals known to have lost their tags is given by the cross-hatched bars.





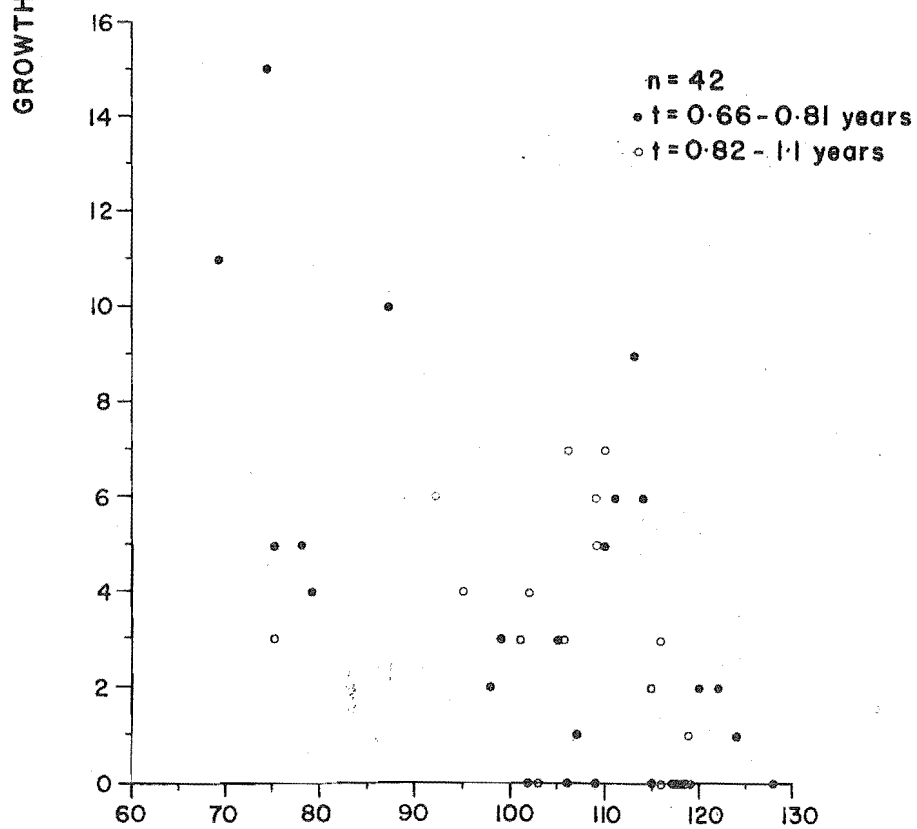
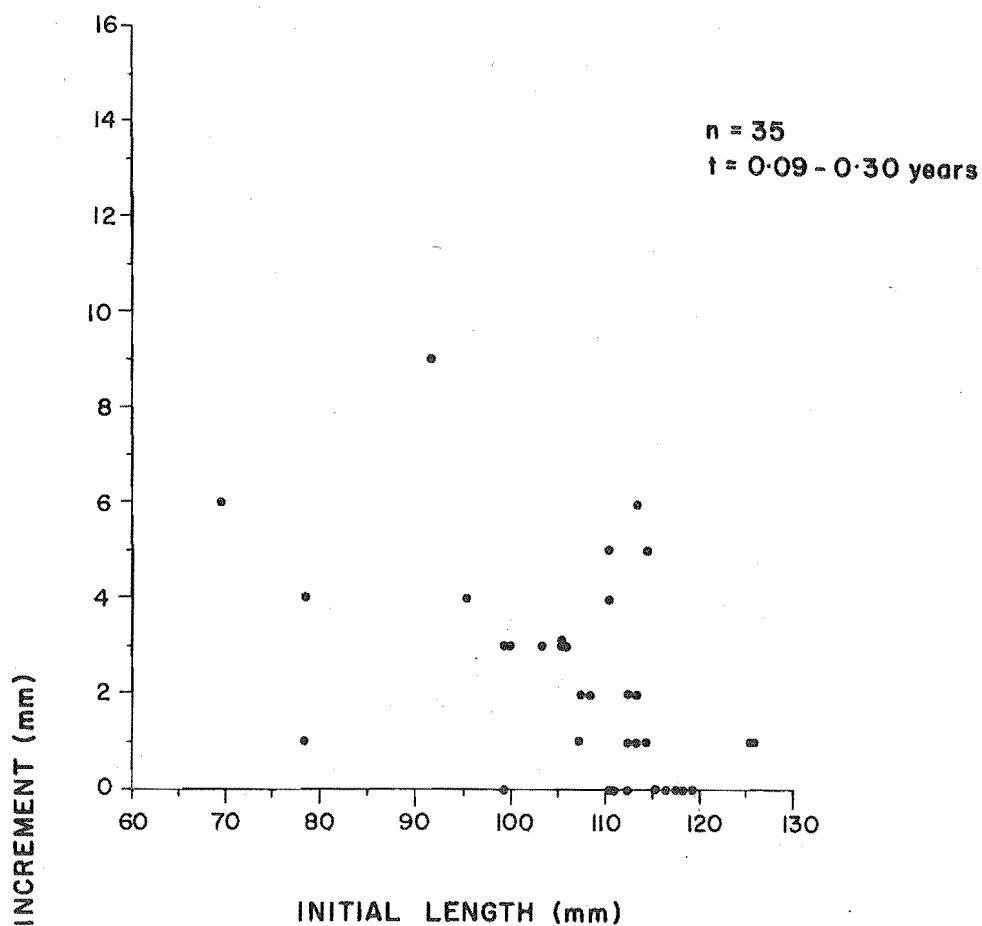
Including multiple recaptures, tag returns provided 77 measurements of the growth increment during a known time interval (see Appendix 3.1). The time at liberty ranged from 33 days (0.09 yrs) to 402 days (1.102 yrs). Scattergrams of growth increment against initial length are shown in Fig. 3.6. Growth was highly variable, and the growth increments measured between February and April (late summer and early autumn) were similar to those obtained from animals which had been tagged for 8-12 months (including the late summer and autumn). Thus, very little growth occurred during the winter, spring and early summer of 1976.

The Von Bertalanffy growth equation in which the time each tagged animal was at liberty is treated as a variable (see Fabens, 1965) was fitted to the recapture data. However, this assumes that growth is uniform in time, and as this was clearly not the case the data were divided into two groups according to whether the time at liberty ( $t$ ) was greater or less than 0.5 yrs. All returns for which  $t$  was less than 0.5 yrs (most values were between 0.15 and 0.3 yrs) were records of growth during the late summer-autumn period and most records for which  $t$  was greater than 0.5 yrs (all values were between 0.66 and 1.1 yrs) included this period. Thus the first group pertains to a period of rapid growth during February, March and April, and the second group should reasonably reflect the annual growth of *H. iris* at Peraki Bay.

Two methods of estimating the growth parameters were applied to each group:

Figure 3.6 Scattergram of growth increment vs. initial length for various times at liberty (t).

The upper scattergram refers to growth during February-April 1976, and the times at liberty for the lower scattergram included this period.



- 1) An unweighted, least squares fit of the Von Bertalanffy equation

$$I = (L_{\infty} - 1) (1 - e^{-Kt})$$

where  $I$  is the growth increment during the time interval  $t$  of an animal with initial length  $l$ . This is the usual method of fitting the Von Bertalanffy equation to tag return data (see Fabens, 1965). Direct least squares estimates were found using the Marquardt algorithm (Marquardt, 1963 and 1966; Conway, Glass and Wilcox, 1970), rather than by the approximate method of Gulland and Holt (1959).

- 2) Maximum likelihood estimates of the parameters of the Von Bertalanffy equation, in which an expression for the variance of the growth increment was included (see Appendix 3.1). The average growth increment ( $I$ ) during time  $t$  of a group of animals of initial length  $l$  is

$$I = (L_{\infty} - 1) \left[ 1 - \left( 1 + \frac{\sigma_K^2 t}{K} \right)^{-K^2 / \sigma_K^2} \right]$$

and its variance is

$$\sigma_I^2 = k_1 \sigma_{L_{\infty}}^2 + k_2 (L_{\infty} - 1)^2$$

where  $k_1$  and  $k_2$  are functions of  $K, t$  and  $\sigma_K^2$  (given in Appendix 3.1). These equations were derived by considering a population consisting of animals growing according to the Von Bertalanffy equation, each with a specific pair of Von Bertalanffy growth parameters.  $L_{\infty}$  and  $K$  are the mean parameter values for the population.  $\sigma_{L_{\infty}}^2$  and  $\sigma_K^2$  express the variation of these parameters among members of the population. Assuming  $I$  is approximately normally

distributed for given initial length and time at liberty, estimates of  $L_{\infty}$ ,  $K$ ,  $\sigma_K^2$  and  $\sigma_{L_{\infty}}^2$  were obtained from the tag return data using the Fletcher-Powell algorithm (see Appendix 3.3). The parameter estimates are given in Table 3.2.

Table 3.2 The parameters of two forms of the Von Bertalanffy growth equation; one in which all individuals in the population are assumed to have identical growth parameters (fitted by the method of least squares (L.S.)), and the other in which the growth parameters vary between individuals (fitted by the method of maximum likelihood (M.L.)). The ninety per cent confidence interval is given in brackets below each estimate.

parameter	time at liberty < 0.5 yr (n=35)		time at liberty > 0.5 yr (n=42)	
	L.S.	M.L.	L.S.	M.L.
$L_{\infty}$ (mm)	133.4 (116.8-150.0)	131.3 (119.1-150.0)	130.0 (116.9-142.8)	131.9 (125.8-164.5)
$K$ (time in yrs)	0.578 (0.231-0.925)	0.6693 (0.447-1.334)	0.171 (0.089-0.253)	0.1636 (0.110-0.338)
$\sigma_K^2$		0.0482 (0.0-0.218)		0.0118 (0.0064-0.0243)
$\sigma_{L_{\infty}}^2$ (mm)		380.6 (253.0-636.8)		138.7 (63.6-294.9)

Similar estimates of  $L_{\infty}$  and  $K$  are provided by both forms of the growth equation. The maximum likelihood estimates are probably the most reliable since the equation fitted takes into account the relationship between the variance of the growth increment and initial length. The large growth increments observed during the autumn of 1976 were mainly a result of the large average value of  $K$  at that time; the average value of  $L_{\infty}$  remains relatively constant throughout the year. The values of  $\sigma_{L_{\infty}}^2$  and  $\sigma_K^2$  during the autumn period are much larger than those obtained

when the year is taken as a whole, suggesting that individuals differ considerably in their ability to take advantage of whatever factors allow rapid growth during the autumn.

The overall relationship between the annual growth increment and initial length, obtained by combining the results of the juvenile and adult analyses, is shown in Fig. 3.7. Annual increments can be obtained from the juvenile analysis for animals up to about 60 mm in length, and the Von Bertalanffy relationship is based on the tag returns from animals over 69 mm in length. From Fig. 3.4 the average length at age 3.2 yrs is 60 mm. And so, putting  $L = 130$  and  $K = 0.17$ , the 'classical' Von Bertalanffy length at age relationship for *H. iris* 3.2 yrs of age and older at Peraki Bay is

$$l_T = 130 - 120.6 e^{-0.17T}$$

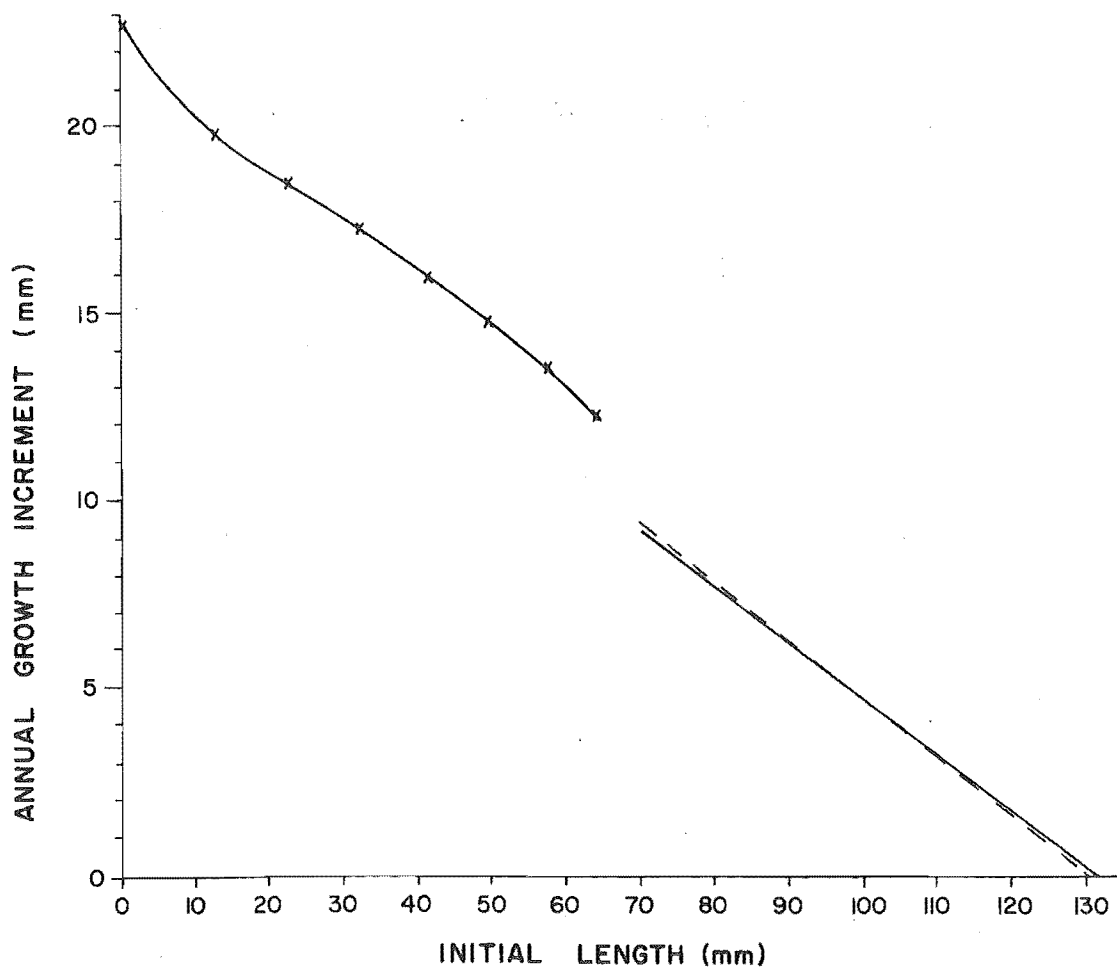
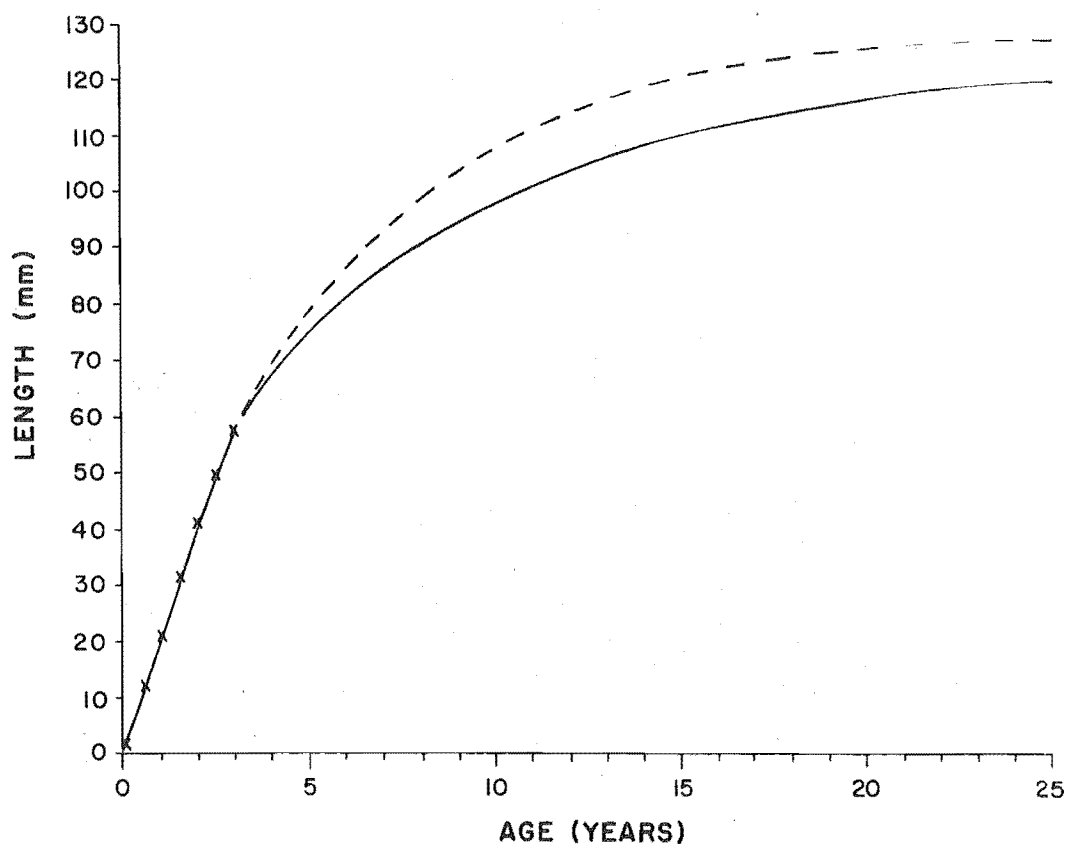
where  $l_T$  is the length in millimetres of an animal  $T$  years old. The corresponding relationship when individual variability of the growth parameters is included (equation vi, Appendix 3.2) is

$$\bar{l}_T = 131.9 \left[ 1 - (1 + 0.07213(T + 1.05))^{-2.2682} \right]$$

where  $\bar{l}_T$  is the average length in millimetres of a cohort of age  $T$ . The predictions of the two equations differ by about 10 mm over the age range 8-20 years (Fig. 3.8). For higher ages ( $> 25$  yrs) this difference progressively decreases as slow growing individuals catch up with faster growing ones.

Figure 3.8 Length at age relationship for *H. iris* at Peraki Bay. Ages for animals less than 60 mm are based on length frequency analysis, and those for larger animals were obtained from tag return data. The dashed line is the classical Von Bertalanffy equation which assumes there is no individual variation of the growth parameters, and the solid line gives the mean size when the growth parameters vary between individuals.

Figure 3.7 Annual growth increment vs. initial length for *H. iris* at Peraki Bay. Increments for animals less than 65 mm were derived from length frequency analysis and those for larger animals were calculated from tag return data. The dashed line is the classical Von Bertalanffy equation, and the solid line is the Von Bertalanffy equation modified to include the effects of individual variability of growth parameters.





These differences are consistent with the remarks made in Appendix 3.2, that the effect of individual variability of  $K$  and  $L_{\infty}$  (of the type examined) is to decrease the mean growth increment for any given initial length (and hence the mean length at any age) relative to the estimates obtained assuming all individuals have identical growth parameters.

### 3.4 DISCUSSION

The tagging method used would not be suitable for longer term studies. After about a year at liberty, tagged animals were difficult to detect under-water because encrusting algae had obscured much of the tag and adhesive. The tag would probably have been completely covered in about six more months, and recognition of tagged animals would then depend upon noticing the unusual bump on the shell. The overall percentage recovery of tagged animals at Peraki Bay was lower than that obtained by Poore (1972c).

Growth of *H. iris* at Peraki Bay differs from that of the Kaikoura population where Poore (1972c) found that  $L_{\infty} = 148.5$  mm,  $K = 0.261$  and  $L_{\infty} = 144.4$  mm,  $K = 0.340$  in two successive years. Abalones at Peraki Bay grow more slowly and reach a smaller maximum size than those at Kaikoura. One year old animals at Peraki Bay are about the same length as one year olds at Kaikoura, but for animals older than two years the difference in growth between the areas becomes increasingly apparent.

The cause of the difference in growth between *H. iris* at Kaikoura and Banks Peninsula is unknown, but possibly

food supply, spawning frequency and irritation caused by sediment are important. Growth is known to be affected by temperature (see Ursin, 1967, for a general discussion and Olsen, 1971, for the effects of temperature on growth of *H. fulgens*). However, *H. iris* populations with the growth characteristics of the Kaikoura population (i.e. large maximum size) are found on Stewart Island, the Otago Peninsula and at Oamaru, where the water is generally cooler than at Banks Peninsula, and also at Wellington where it is generally warmer (Garner, 1969). Thus it is unlikely that small maximum size in *H. iris* at Peraki Bay is attributable to suboptimal water temperatures. The localised nature of the phenomenon also suggests that it is not caused by genetic differences between stocks since the planktonic larval stage allows genetic exchange between widely separated populations (larval dispersal is discussed in Chapter 5). However, the opportunities for feeding and the quality of the food species available to abalones on Banks Peninsula may be poorer than those at Kaikoura. Poore (1972a) has noted that, given a choice, *H. iris* prefer red algae to brown, and juvenile animals kept by him in the laboratory for six months grew faster when fed the red algae *Hymenocladia lanceolata* than when given the brown algae *Lessonia variegata*. The average growth rate of 30 individuals fed *Hymenocladia* was 3.1 mm per month whereas the same number of animals fed *Lessonia* grew, on average, 0.33 mm per month. Poore reported that growth rate under field conditions was 3.0 mm per month. On Banks Peninsula, where red algae are rare, the abundant brown alga *Macrocystis pyrifera* is the main

food species. If the difference in growth rate which Poore observed when abalones were fed *Hymenocladia* and *Lessonia* in the laboratory is general for red and brown algae under field conditions, the scarcity of red algae on Banks Peninsula could be a contributing factor to the slower growth rate of *H. iris* there. Furthermore, the algae at Peraki Bay may be less available to abalones than is the case at Kaikoura. Several haliotids, including *H. iris*, have been shown to feed extensively on drift algae (Cox, 1962; Leighton and Boolootian, 1963; Poore, 1972a; Shepherd, 1973a), and *H. iris* at Peraki Bay were often observed catching drifting *Macrocystis*. Shepherd has shown that there is a particular level of water movement associated with the optimal feeding rates of *H. laevis* and of *H. ruber*; during very heavy wave action most drift algae are transported high in the water column, beyond the reach of abalones, whereas during calm conditions pieces of algae are not broken off living plants by waves, and drift algae already present are not transported to the sedentary abalones. Although no quantitative data are available, wave action within the bays on Banks Peninsula is generally not as strong as at Kaikoura, and so the rate of delivery of food to the Banks Peninsula abalones may be limiting individual growth.

A further possible cause of slow growth of *H. iris* on Banks Peninsula is the high silt load of the water in this region. *H. iris* on Banks Peninsula probably expend more energy maintaining clean gill surfaces, and ingest more sediment than do their counterparts in areas with a lighter

silt load. Irritation caused when this sediment is trapped between the mantle and shell may be partly responsible for the high incidence of shell abnormalities among *H. iris* on Banks Peninsula (see Chapter 6), suggesting that the high silt load may affect the growth process directly, possibly by preventing or modifying the activity of secretory cells in the mantle.

Variability of the growth parameters between localities has been demonstrated for other haliotids. From the results of a tagging study in Guernsey, Forster (1967) found that the growth parameters of *H. tuberculata* from two different habitats only about 60 m apart were  $L_{\infty} = 101.5$  mm,  $K = 0.4$  and  $L_{\infty} = 97.9$  mm,  $K = 0.33$ . Population density was lower and algal food supplies were more abundant in the habitat where growth rate and asymptotic size were greatest. Leighton and Ecolootian (1963) showed that the growth rate of *H. cracherodii* was considerably lower in an area where marine algae were rare than in an area supporting a diverse and abundant flora. They stated that "variability of growth rate seems a rule rather than an exception" in *H. cracherodii*. Poore (1972c) found that the values of  $L_{\infty}$  and  $K$  for *H. virginea* at Kaikoura and Stewart Island were 61.5 mm, 0.446 and 64.3 mm, 0.323 respectively. Harrison and Grant (1971) found that  $L_{\infty}$  for a population of *H. ruber* occupying a relatively sheltered site was 160 mm, whereas for a population in an exposed area  $L_{\infty}$  was 175 mm. The values of  $K$  were 0.22 and 0.24 respectively. Shepherd and Laws (1974) reported that both *H. ruber* and *H. laevigata* grew faster, at least during the

first three years of life, in exposed areas than in sheltered areas. At three years of age, *H. laevigata* from an exposed shore were, on average, 30 mm larger than those from a sheltered shore, whereas for *H. ruber* this difference was 23 mm.

Thus it would seem that the most likely causes of low growth rate and asymptotic size of *H. iris* at Peraki Bay are the poor quality (and possibly diversity) of the algal food species present, combined with a slow rate of delivery of drift algae due to the relatively low level of water movement.

Growth of *H. iris* varies seasonally at Peraki Bay and possibly also at Kaikoura (Poore, 1972c). Poore's seasonal growth data for 1968 are presented in Table 3.3. The seasonal parameters are not significantly different.

Table 3.3 Seasonal values of the Von Bertalanffy growth parameters of *H. iris* at Kaikoura (from Poore, 1972c). The values of K assume time is expressed in years.

Season	K	$L_{\infty}$ (mm)
Autumn	0.328	153.6
Winter	0.208	143.5
Spring	0.312	145.3
Summer	0.272	156.6

Growth appears to be fastest during autumn at both Kaikoura and Peraki Bay, but the magnitude of the seasonal difference is greater at Peraki Bay. Seasonal differences in the growth rate have been recorded for other haliotids (see Table 3.4), and for two species the magnitude of the seasonal difference appears similar to that found for *H. iris*

Table 3.4 The spawning season and period of most rapid growth of various haliotid species

Species	Period of most rapid growth	Usual spawning season	Author
<i>H. tuberculata</i>	autumn	summer	Forster (1967)
<i>H. rufescens</i>	winter	summer	Cox (1962)
<i>H. midae</i>	winter and spring	early summer and early autumn	Newman (1968)
<i>H. discus hannai</i>	spring and summer	autumn	Sakai (1962)
<i>H. cracherodii</i>	summer	spring to autumn	Leighton and Boolootian (1962)
<i>H. iris</i>	spring and autumn	autumn	Poore (1972c,d)
	autumn	autumn	Present study

at Peraki Bay. Forster (1967) found that *H. tuberculata* grew very little during the winter and early summer whereas many individuals grew about 70% of their annual increment in a single autumn month. Cox (1962) reported that almost the entire annual increment of *H. rufescens* was attained during the winter.

The pattern of seasonal growth observed at Peraki Bay during 1976 may not occur every year because the rapid growth during the autumn may be related to the spawning failure of the Peraki Bay population at this time (see Chapter 4). Since the recovery of the gonad after spawning would probably require a considerable amount of energy, the growth rate may be expected to decrease following spawning. The time of spawning and period of maximum growth of several haliotid species are given in Table 3.4. There appears to be a tendency in some species (including *H. iris*)

for the period of maximum growth to be during or directly preceding the spawning season, and for the growth rate to be lowest following spawning. Sakai (1962) found that the growth rate of laboratory reared *H. discus hannai* decreased during recovery of the gonad following spawning. In *H. iris* and *H. midae*, immature animals in the field showed slow growth rates at the same times as mature animals, suggesting that factors other than the energy requirements of rapid gonad production may be involved in causing the decreased growth rate after spawning (Poore, 1972c; Newman, 1968). Despite this possibility, the failure of spawning would probably allow a greater expenditure of energy on growth than would be possible had spawning occurred. Thus the annual growth rate of abalones at Peraki Bay during years in which the population spawns may be lower than that recorded during this study, and the very rapid autumn growth may occur only when spawning fails. Although tagging studies would have to be continued for several years to clarify this point, collaborating evidence is provided by Poore (1972c,d). *H. iris* at Kaikoura did not spawn in the autumn of 1969 and the value of K for that summer-autumn (6 month) period was 0.415, whereas for the summer-autumn of the previous year (when the population did spawn) K was 0.293. If growth at Peraki Bay during the winter and early summer of 1976 was typical of growth during the whole of a 'spawning' year, and if spawning occurs every second year, then the overall value of K for *H. iris* at Peraki Bay could be about 0.1.

The values of K reported for *H. iris*, 0.31 at Kaikoura and 0.17 at Peraki Bay, are within the range given for other haliotid species. Values of K for *H. australis* and *H. virginea* are between 0.32 and 0.46, whereas those for *H. tuberculata* and *H. discus hannai* are between 0.3 and 0.4 (see Poore, 1972c). Newman (1968) found that  $K = 0.059$  for *H. midae*, and Harrison and Grant (1971) give values of 0.22 to 0.24 for *H. ruber*.

The theoretical treatment of growth presented in Appendix 3.2 of this chapter results from a superficial examination of the effects of individual variability of growth parameters on the description of growth for a group of animals. A more detailed examination was not possible in the time available. However, the present treatment suggests that biased estimates of the mean values of  $L_{\infty}$  and K for a group of animals are obtained by fitting the Von Bertalanffy curve, as derived to describe individual growth, to tag return data. The bias results from individual variability of the growth parameters. Ignoring this individual variability (i.e. using the growth equation for an individual to describe the growth of a group) can result in serious overestimates of the mean length at age of a cohort. Future work in this field is planned, using laboratory populations, which will allow a more critical examination of growth than was possible here, particularly with respect to the distributions of  $L_{\infty}$  and K and the resulting distribution of the growth increment for given initial length.



#### 4. REPRODUCTION AND RECRUITMENT

##### 4.1 INTRODUCTION

The level and pattern of recruitment (the number of young surviving to enter a stock) and their response to changes in population density are extremely important aspects of the dynamics of an exploited population, and as such have received much theoretical attention, e.g. Beverton and Holt (1957), Ricker (1954), Larkin, Raleigh and Wilimovski (1964), Larkin (1973) and Paulik (1973). In most fish populations studied, changes in stock density have a greater effect on reproduction and recruitment than on any other population parameter (Cushing and Harris, 1973), often to such an extent that the other parameters may reasonably be treated as constants (cf. Allen and Basaisbwaki, 1974). Unfortunately, the recruitment to a population is usually very difficult to measure. Even when it is possible, many years of surveillance may be necessary before sufficient data from a wide enough range of stock densities are collected to enable the examination of density dependence.

No estimates of recruitment have been published for any haliotid population, but reproductive cycles and the number of eggs present in ripe gonads (hereafter referred to as fecundity, see Bagenal, 1973) have been recorded for a number of species. These are fully reviewed by Poore (1972d) and Shepherd and Laws (1974) and reveal great variability

both within and between species. In all species studied, however, the sexes are separate with development proceeding from external fertilization through free swimming trochophore and veliger stages.

The reproductive cycle and size specific fecundities were determined for *H. iris* at Peraki Bay, and recruitment to the population during two years was estimated.

## 4.2 METHODS

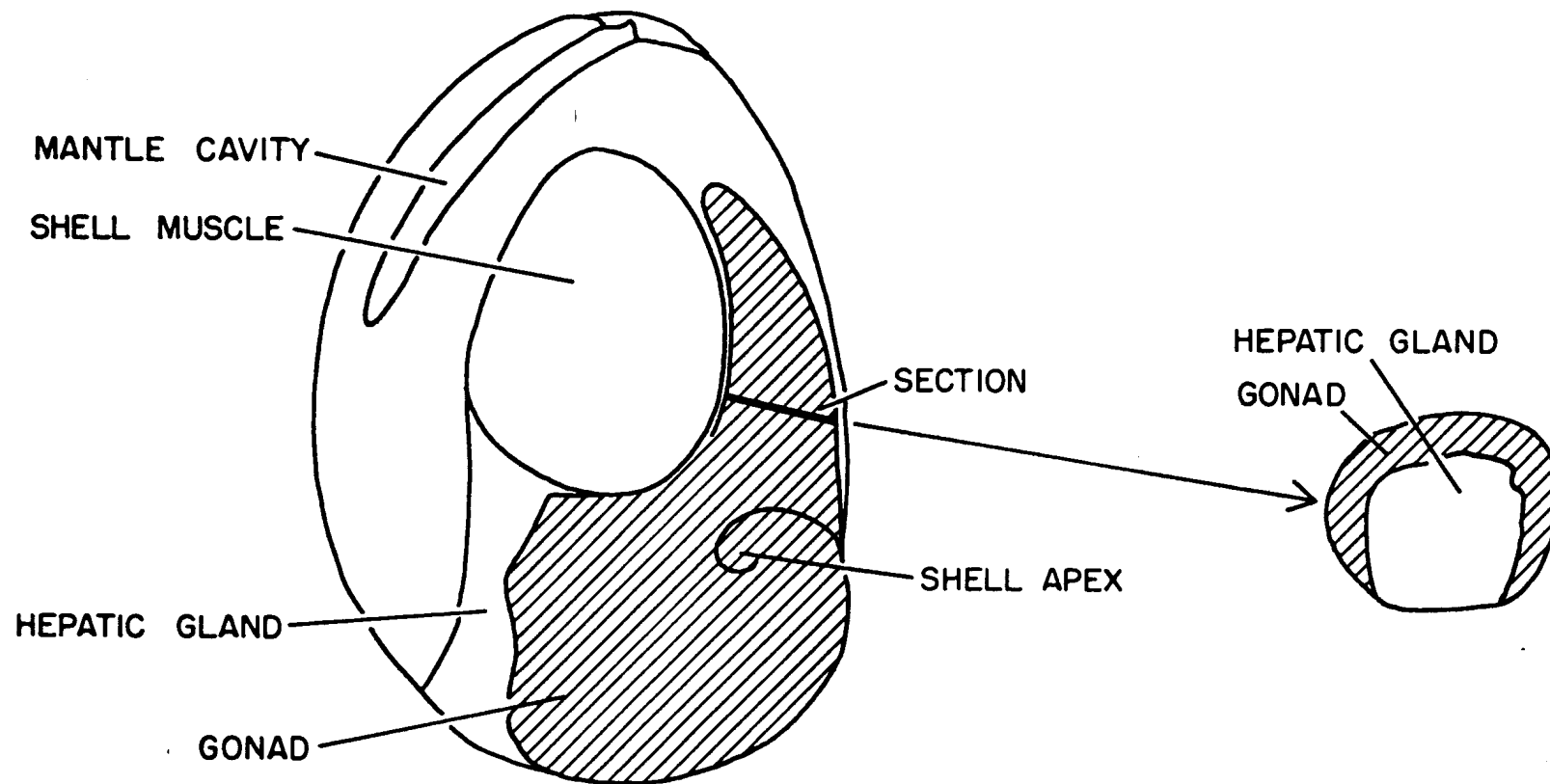
### 4.2.1 Reproduction

The reproductive cycle was examined by means of the gonad index described by Poore (1972d). The entire stomach, hepatic gland and gonad of animals collected for gonad index estimation were preserved and hardened in 10% formalsaline, and transversely sectioned at a point one third the distance from the tip of the gonad to the shell apex (Fig. 4.1). An 8.5× magnification, outline drawing of the cross-section was made using a camera-lucida mounted on a binocular microscope. The parts of the drawing representing gonad and hepatic gland tissue were cut out and weighed to obtain the proportionate gonad area of the original cross-section. The gonad index was then calculated as

$$\text{gonad index} = \frac{\text{gonad area}}{\text{total section area}} \times 100$$

To test for spatial differences in maturation within the population, gonad indices were calculated for ten 110-115 mm animals collected in November 1973 from each of four strata (EJ, WJ, EA and WA) defined in Chapter 2.

Figure 4.1 Dorsal view of *H. iris* with shell removed  
to show the position of the section used to  
calculate the gonad index.



The null hypothesis that there is no difference in gonad index between strata was accepted after analysis of variance ( $F = 0.16$ , d.f. = 3,37).

To examine the relationship between length and gonad index, fifty-one animals, ranging in size from 75 mm to 130 mm, were collected from the EJ stratum in February 1974 and their gonad indices were calculated. Since the gonad index did not alter appreciably with length over the range 105 to 120 mm (see Fig. 4.2) eighteen samples of from seven to twenty-five individuals within this size range were collected between May 1975 and April 1976 to monitor spawning activity. Animals were collected from the EJ and EI strata, and since Poore (1972d) had established that spawning of *H. iris* occurs between February and early April, sampling at Peraki Bay was concentrated around the mid-summer to late autumn months.

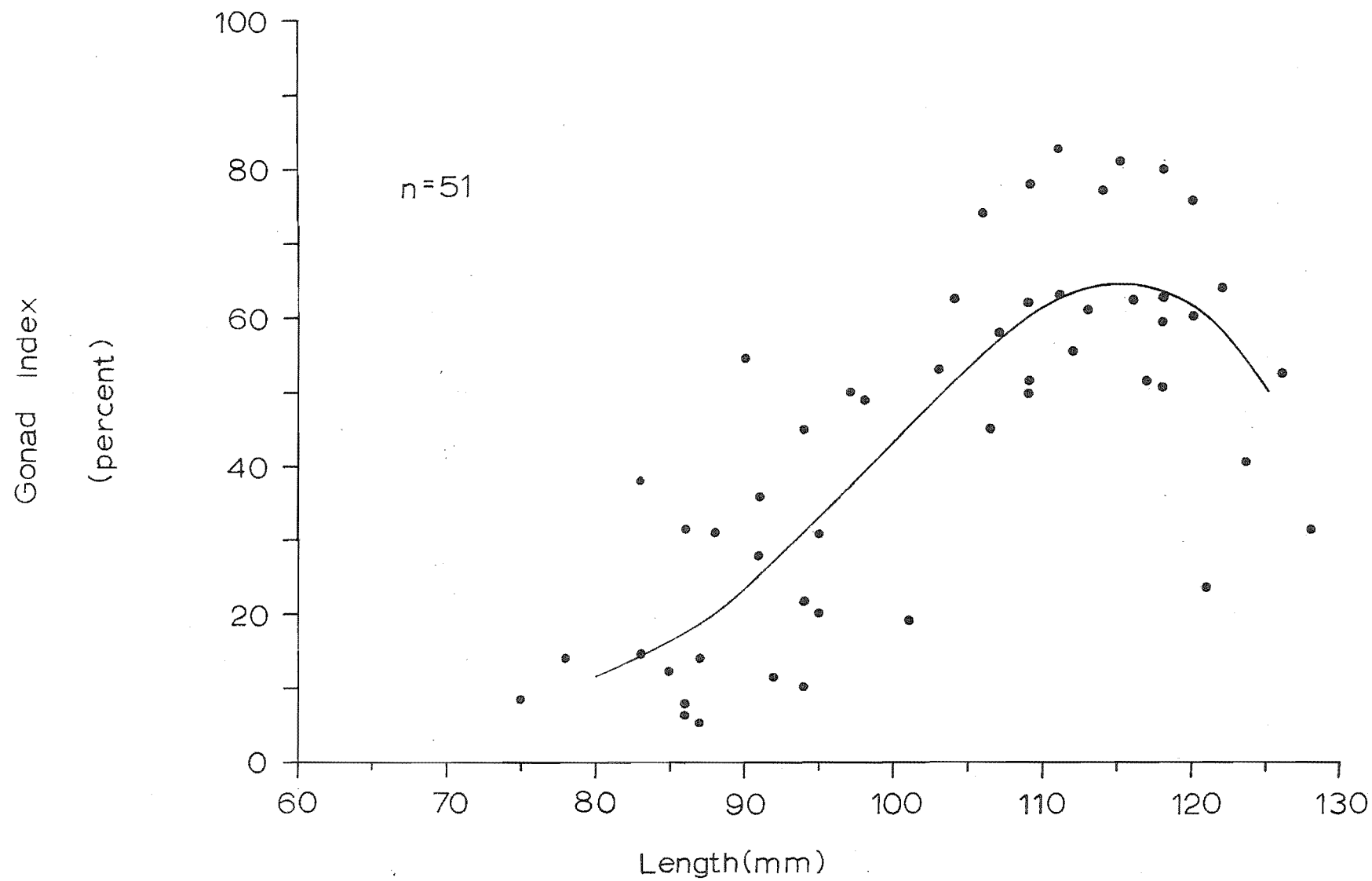
The condition of abalone gonads (i.e. ripe/spawned) collected in late autumn from areas other than Peraki Bay was determined when the opportunity arose. In May 1974, fifteen gonads from Kaikoura and twelve from Menzies Bay (on the northern end of Banks Peninsula) were examined. During May and June 1976, ten gonads from Kaikoura, fifteen from Taylors Mistake (on the northern coast of Banks Peninsula), sixteen from Oamaru, and eighteen from the Otago Peninsula were examined.

Fecundity was estimated for each of 35 females within the size range 70 to 140 mm collected from throughout Peraki Bay during February 1976. The viscera of each animal were hardened in 10% formalsaline and the gonad dissected from the hepatic gland.

Figure 4.2 Gonad index vs. length in February 1974.

The least squares regression line relating the gonad index (G.I.) to length (L) in millimetres is

$$\text{G.I.} = 2048.1 - 65.987 L + 0.69711 L^2 - 0.002376 L^3$$



The gonad was gently broken up into approximately 100 ml of sea water and agitated mechanically until all eggs were free (this required at least 24 h). Three or four 1.0 ml samples were taken and the total number of yolky eggs in each sample counted (Poore, 1972d, found that yolky eggs were spawned while the smaller, stalked eggs were not). The fecundity of each animal was calculated by multiplying the average number of eggs per ml by the total volume of the egg-seawater suspension.

The sex ratio was determined from the 616 animals sexed during the course of this study. The first 314 of these were sexed both by microscopic examination and by noting the colour of the gonad. Poore (1972d) found that males had cream gonads, whereas gonads of females were deep green. Although the gonads of females from Peraki Bay were often very light green-cream, sexing by the colour of the gonad proved reliable in 98% of cases. Therefore, the remaining 302 animals were sexed in this way alone.

#### 4.2.2 Recruitment

Recruitment of 1+ year old animals to the Peraki Bay population in February 1974 and February 1976 was estimated from the results of the transect sampling programme described in Chapter 2. (Since the 1+ year class is almost 2 years old in February, henceforth they will be referred to as two year olds.) The number of two year olds, identified on the basis of length, within each transect sample was counted and the total recruitment to Peraki Bay was estimated from these data using the method described by Seber (1968) and summarised in Chapter 2. Two year old



animals ranged in size from 24 to 56 mm (mean  $\pm$  2 standard deviations) in February 1974 and from 34 to 54 mm in February 1976 (see Chapter 3). This method of ageing is inexact because:

i) The mean and variance of the length of two year olds are not known exactly (nor in fact is the form of the distribution).

ii) The length frequency distributions of 1, 2 and 3 year old animals overlapped. There was pronounced overlap in the size range of 1 and 2 year olds in February 1976, but in all other cases the degree of overlap was slight.

Both of these problems are compounded by the low numbers of juveniles encountered during sampling, so the estimates of recruitment must be treated as approximate.

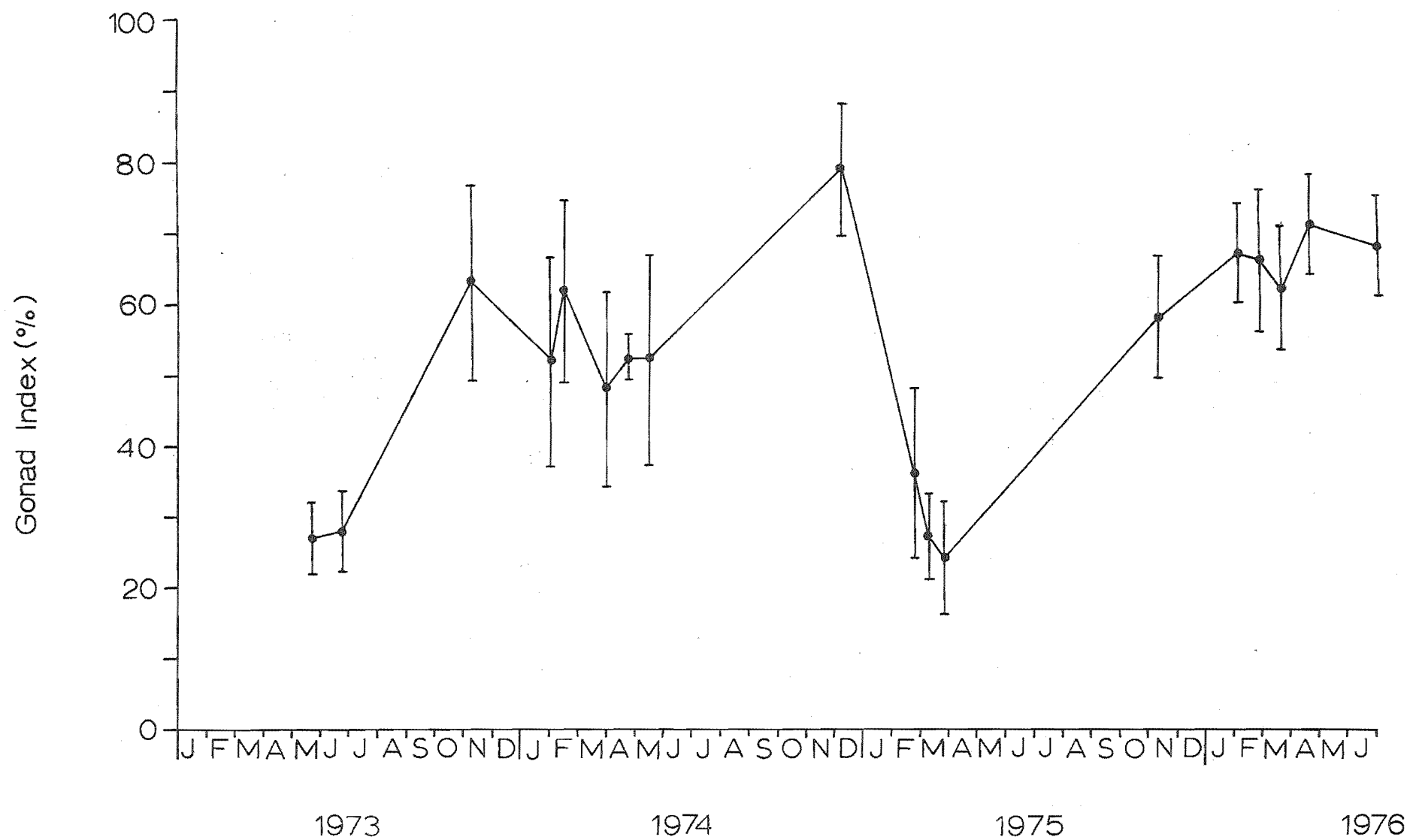
To examine the relative strengths of recruitment to Kaikoura during 1974 and 1975, juvenile *H. iris* were collected from Laboratory Rocks, Kaikoura (see Poore, 1972c) on 20 February 1976. Both the intertidal and subtidal zones were searched along about 20 m of coastline.

## 4.3 RESULTS

### 4.3.1 Reproduction

The mean gonad index of animals within the size range 105-120 mm is plotted against time in Fig. 4.3. The population had already spawned when sampling began in May 1973 (as indicated by the low initial gonad index) and had recovered by November of the same year. The pattern during 1974 differed markedly from that of 1973.

Figure 4.3 Change in gonad index with time. A sudden decrease of gonad index is associated with spawning. Points are the mean gonad index, and vertical bars indicate  $\pm$  two standard errors.



There was no significant change in the gonad index between November 1973 and May 1974 (analysis of variance,  $F = 1.22$ , d.f. = 5,50), suggesting that the population did not spawn. However, of the fifty-five animals examined between February and May 1975, four individuals (two in February and two in March) had spent gonads (indices of 20, 22, 26 and 33), suggesting that some animals in the population (possibly about 7%) had spawned. All abalones examined in May 1974 from Menzies Bay had full gonads, indicating that the low spawning rate found at Peraki Bay was typical of the Banks Peninsula region. However, spawning must have occurred 'normally' at Kaikoura because all gonads collected there in May 1974 were spent.

The gonad index at Peraki Bay increased further during the following winter and then decreased suddenly between late December 1974 and February 1975, indicating that the Peraki Bay population had spawned. Since the gonad index continued to drop between February and April 1975, it appears that all individuals do not release all of their gametes simultaneously. The gonad index increased during the winter of 1975, but the population failed to spawn in 1976. None of the 62 animals examined between February and April 1976 was found to have spent gonads. Similarly, all animals examined in May and June 1976 from Kaikoura, Oamaru, Otago Peninsula and Taylors Mistake still had full gonads. Thus, in contrast to the 1974 pattern, the failure to spawn in 1976 was widespread (see Table 4.1).

Table 4.1 Reproductive activity of *H. iris*. + indicates spawning; - indicates a failure, or partial failure, of spawning and a blank indicates no record. The 1968 and 1969 records are from Poore (1972d).

Year	Kaikoura	Banks Peninsula	Oamaru	Otago Peninsula
1968	+	+		
1969	-	-		
1973		+		
1974	+	-		
1975		+		
1976	-	-	-	-

Of the 616 mature animals (i.e. animals in which the gonad was sufficiently developed to allow sex to be determined) examined from Peraki Bay, 210 were males and 406 were females. This sex ratio is significantly different from 1:1 ( $\chi^2 = 62.3$ , d.f. = 1). Of the total sample, 410 were collected during the transect sampling programme in February 1976, and these records were divided into those collected on the eastern and western sides of the bay. A test of homogeneity on the table

	males	females
Eastern coast	116	182
Western coast	64	48

detected a significant difference in the distribution of the sexes ( $\chi^2 = 10.79$ , d.f. = 1). The sex ratio on the eastern shore is significantly different from 1:1 ( $\chi^2 = 14.61$ , d.f. = 1), while that on the western shore is not ( $\chi^2 = 2.28$ , d.f. = 1). The sex ratio on the eastern shore is about 2:3: males : females.

The relationship between fecundity and total shell length in February 1976 is shown in Fig. 4.4. Polynomials higher than the cubic shown in Fig. 4.4 do not significantly reduce the mean square error further, although the variability in fecundity between animals is so great that the use of any regression line is questionable. Figs 4.3 and 4.4 show that both the gonad bulk and fecundity increase rapidly with length for animals about 90 to 100 mm long, which probably denotes the beginning of effective reproduction. Although some animals as small as 70 mm produced eggs, their fecundity was very low and their contribution to the total population's egg output, assuming animals of this size could in fact spawn, would be negligible.

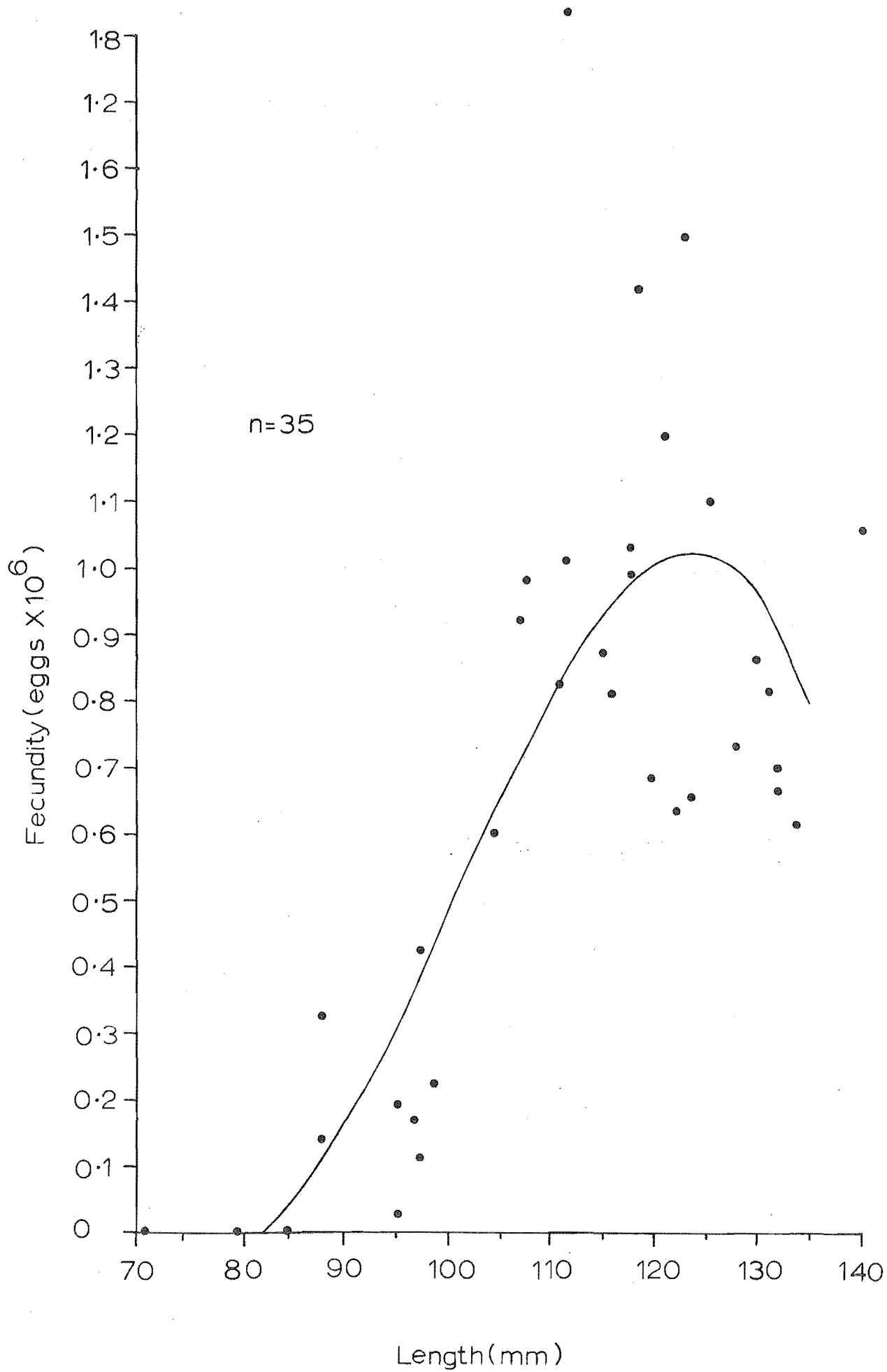
Table 4.2 gives the egg production of the Peraki Bay population based on the fecundity-length relationship shown in Fig. 4.4 and the population length structure established in Chapter 2. If it is assumed that the fecundity of the 130-140 mm females remains at  $10^6$ , rather than decreases as shown in Fig. 4.4, the estimate of total egg production is increased by less than 1%.

Table 4.2 Egg production of the Peraki Bay *H. iris* population. The male : female sex ratio was taken to be 2:3 on the eastern shore and 1:1 on the western shore.

Size range (mm)	Eastern shore		Western shore	
	No. females	No. eggs ( $\times 10^6$ )	No. females	No. eggs ( $\times 10^6$ )
81 - 90	5 915	190.1	967	31.1
91 - 100	14 586	4 658.9	1 001	319.8
101 - 110	25 581	16 973.6	5 095	3 380.8
111 - 120	26 293	24 703.2	6 902	6 484.4
121 - 130	5 973	6 123.2	8 156	8 360.7
131 - 140	1 155	920.1	2 511	2 000.1
		31 269.1		20 576.9
Total egg production = $5.184 \times 10^{10}$				

Figure 4.4 Fecundity (egg content) vs. length for female *H. iris* at Peraki Bay in February 1976. The least squares regression line relating fecundity (F) in millions of eggs to length (L) in millimetres is

$$F = 17.3339 - 0.57772 L + 0.006153 L^2 - 0.0000206 L^3$$





#### 4.3.2 Recruitment

The number of two year old *H. iris* (24 to 56 mm in 1974, 34 to 54 mm in 1976) in each of the transect samples taken from the EJ, EI and WJ strata is given in Table 4.3. Two year olds did not occur in samples taken from the remaining strata.

Table 4.3 Number of two year old (24-56 mm in 1974, 34-56 mm in 1976) *H. iris* in each of the transect samples. \* Denotes a juvenile-only transect.

Year	Stratum	Number of transects	Number of two year olds	Total
1974	EJ	7	1*,2*,3*,7*,6*,4*,3*	26
	EI	6	5, 1, 1, 6, 7, 2	22
	WJ	7	0*,5*,3*,6*,3*,4*,0*	21
				69
1976	EJ	10	2, 0, 1, 2, 1, 3*,4*,1*,6*,6*	26
	EI	3	3, 0, 2	5
	WJ	3	0, 2, 1	3
				34

The null hypothesis that "the 1974 and 1976 samples were drawn from populations with equal numbers of two year old animals" was examined using a two-way analysis of variance (years vs. strata) in which each stratum was weighted according to the proportion of the available coastline occupied by that stratum. The hypothesis was accepted ( $F = 3.43$ , d.f. = 1,30).

The estimates of the number of two year old *H. iris* in Peraki Bay during February 1974 and February 1976 are given in Table 4.4. The standard deviations of the estimates are based on sampling variability and do not include the effects of incorrect assignment of age.

Table 4.4 Estimated total number of two year old *H. iris* in Peraki Bay in February 1974 and February 1976. Based on Table 4.3.

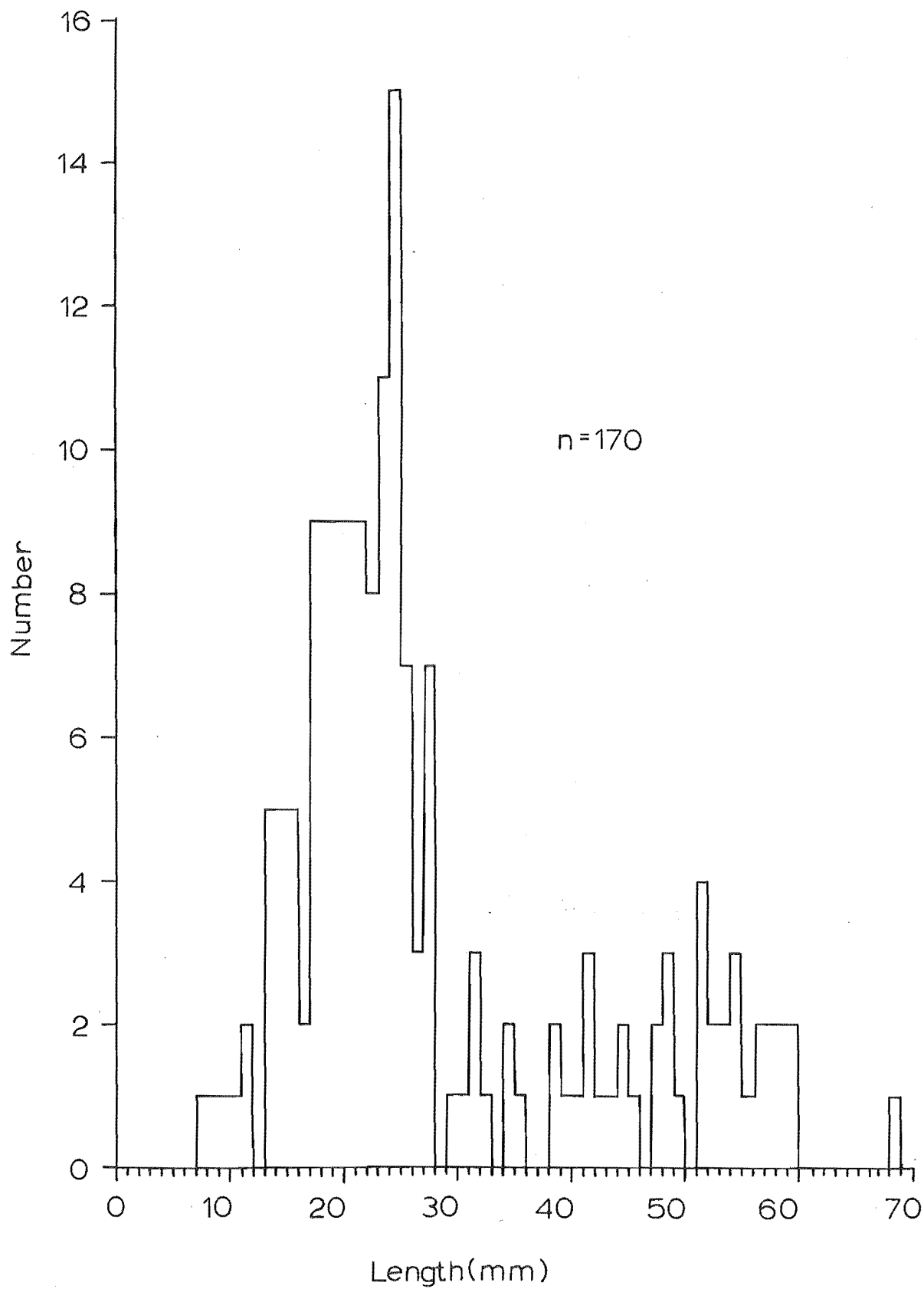
Year	Stratum	Length of coastline(m)	Number of transects	Number per transect	Total number	Standard deviation
1974	EJ	110	7	3.71	408	86
	EI	900	6	3.66	3 300	976
	WJ	510	7	3.00	<u>1538</u>	442
					5 238	1 072
1976	EJ	110	10	2.60	286	70
	EI	900	3	1.66	1 500	792
	WJ	510	3	1.00	<u>510</u>	293
					2 296	847

The length frequency distribution of the animals collected at Kaikoura in February 1976 is shown in Fig. 4.5, and is comparable with Fig. 1 of Poore (1972c). From Poore's results, animals between about 10 mm and 30 mm are considered to be one year olds, whereas animals between 30 mm and 60 mm are predominantly two year olds. On the basis of this one sample it appears that recruitment to the Kaikoura population from the 1974 spawning was low, but that a strong year class resulted from the 1975 spawning.

#### 4.4 DISCUSSION

The reproductive 'cycle' of *H. iris* is very irregular. Spawning occurred in only two of the four potential spawning seasons within the period of the present study, and in only one of the two seasons monitored by Poore (1972d).

Figure 4.5 Length frequency of *H. iris* less than 70 mm  
at Laboratory Rocks, Kaikoura, in February 1976.



The cause of this variability in spawning is unknown. Ino (1952) showed that the seawater temperature must reach 20°C before *H. discus* may spawn, but Webber and Giese (1969) found no evidence to suggest that either sea temperature or photoperiod synchronised spawning in *H. cracherodii*. Poore (1972d) considered that differences in seawater temperature between 1968 and 1969 were not responsible for the spawning failure at Kaikoura in 1969. Cox (1962) found that *H. rufescens* did not produce gametes for three years following the destruction of their main algal food supply by an unseasonal influx of warm water. Annual differences in food availability are unlikely to be responsible for spawning failures in *H. iris* since gonad development both at Kaikoura and Banks Peninsula seems to proceed normally during 'non-spawning' years (i.e. yolky eggs are produced).

The sex ratio of about one male to two females found at Peraki Bay differs from that previously recorded for *H. iris*, although it is consistent with Comforts' (1957) suggestion that females predominate in populations of long-lived molluscs. Poore (1972d) examined 494 animals from Kaikoura and 335 from Taylors Mistake, and the sex ratio did not differ significantly from 1:1 in either sample. Sinclair (1963) examined 598 animals from Wellington and found significantly more males than females. However, since the sex ratio is different on the two sides of Peraki Bay, the sex ratios given for the Kaikoura and Wellington regions may only reflect the sex ratios in localised sampling areas within these regions. Newman (1967) determined the sex ratio of *H. midae* at three localities. At two of these the sex

ratio did not differ significantly from 1:1, but significantly more females than males were found at the third. Shepherd and Laws (1974) found that females were significantly more numerous than males in old populations of *H. laevigata* and *H. scalaris*, whereas in *H. ruber* males predominated. They also stated that behavioural differences between the sexes caused males to be more available to sampling than females, which may bias sex ratio estimates based on casual collections. Sex ratios of 1:1 have been recorded for *H. cracherodii*, *H. rufescens* and *H. tuberculata* (Webber and Geise, 1969; Boolootian *et al.*, 1962; Crofts, 1937 respectively).

The relationship between fecundity and body length found at Peraki Bay differs from that reported for *H. iris* from Kaikoura (Poore, 1972d) in two important respects:

- 1) The fecundity of animals from Peraki Bay is considerably lower than that from Kaikoura. For example, a 120 mm female from Kaikoura contains about two million eggs, whereas one from Peraki Bay contains about one million.

- 2) At Peraki Bay individual fecundity reaches a maximum in animals about 120 mm long, with animals larger than 130 mm exhibiting slight reproductive senility. Poore (1972d) found that the fecundity of *H. iris* from Kaikoura continued to increase with increasing length, although he did note that "there is a slight tendency for gonad indices, and from this fecundities, to be slightly lower in the largest females".

The causes of these differences are unclear, although the lower food rations and higher water sediment load experienced by Banks Peninsula abalones (discussed with respect to growth in Chapter 3) could be important. The relationship between fecundity and body size has been established for two other haliotids, *H. australis* (Poore, 1972d) and *H. midae* (Newman, 1968), and in neither case is there evidence of reproductive senility in large females.

In comparing the Banks Peninsula and Kaikoura populations, it is interesting to note that there is no reduction in size at first maturity to compensate for the lower overall fecundity and slower growth rate of abalones on Banks Peninsula. In both populations egg production begins in females about 90 mm in length.

The estimated recruitment of two year olds to Peraki Bay in 1974 did not differ significantly from that in 1976, and the population structure in February 1976 (Figs. 2.4 and 2.5) indicates that a similar number of recruits entered the population in 1975. Thus the recruitment to Peraki Bay was essentially constant during the three year period despite differences in the spawning success of local adults during two of the spawning seasons responsible for the recruitment (total spawning in 1973, low spawning rate in 1974). Recruitment to the Kaikoura population followed the pattern of spawning success observed on Banks Peninsula, i.e. recruitment to the Kaikoura population from the 1974 spawning was poor, whereas recruitment from the 1975 spawning was very good, despite the failure to spawn of Kaikoura adults in 1975.

Although no conclusions may be drawn on so few data (the apparent pattern could easily be due to chance combinations of events), the information available suggests that recruitment is weakly dependent on the spawning success of local adults and/or is related by a highly variable process.

Although no recruitment data for other haliotid populations are available for comparison, the estimates of recruitment to Peraki Bay are lower than would usually be expected for a mollusc population of about 179,000 individuals. There are three possible interpretations of the low recruitment estimates, and it must be noted that they are not mutually exclusive.

i) Recruitment during the period of study was well below the long-term average level required to maintain the observed stock. It is well known that recruitment, particularly of a species possessing a planktonic larval phase, may vary greatly in both space and time, and Poore (1972d) has noted for *H. iris* at Kaikoura that "spawning and ...spatfall vary remarkably from year to year".

ii) The mortality rate of *H. iris* is extremely low, and so a large input of recruits is unnecessary. Assuming steady state conditions, a recruitment of about 2000 to 5000 two year olds per year to a population of about 179,000 individuals implies that about 97% to 99% of that population survive annually. This is discussed further in Chapter 6.

iii) The numbers of two year old animals present were grossly underestimated by their being overlooked during sampling. However, this is unlikely to be an important source of error as each transect was searched very



thoroughly and a consistent temporal trend was found in the population structure of a repeatedly sampled stratum (the eastern intermediate stratum, Fig. 2.6). Furthermore, even if the estimated recruitment is trebled, comments (i) and (ii) above are altered very little.

## 5. LARVAL DISPERSAL

### 5.1 INTRODUCTION

The development of *Haliotis iris* up to and including the veliger stage was described by Poore (1969). This description does not differ greatly from those published for other haliotid species (Croft, 1937, for *H. tuberculata*; Murayama, 1935, for *H. gigantea*; Carlisle, 1945, for *H. rufescens*; Ino, 1952, for *H. sieboldii* and *H. discus*; Leighton, 1972, for *H. sorenseni*), suggesting that development proceeds in much the same way throughout the genus. Thus it is likely that *H. iris* could remain planktonic for 5-10 days (see Poore, 1969), although the longer larval duration may occur only when suitable settlement sites are unavailable.

While there are several descriptions of development little has been published concerning larval behaviour. During rearing experiments, Murayama (1935) noted that trochophores of *H. gigantea* actively maintained station in the upper few centimetres of the water column, and Ino (1952) described the same phenomenon for the veligers of *H. sieboldii* and *H. discus*. Leighton (1972) found that the trochophore of *H. sorenseni* exhibited a strong negative geotaxis, but the veligers swam throughout the water column of his culture vessels. Poore (1969) reported a strong negative geotaxis throughout the trochophore and at least the early veliger stages for *H. iris*.

If such behaviour is typical of *H. iris* larvae under field conditions one would expect them to be transported by ocean surface currents for much of their larval lives. Therefore, an understanding of the surface current system within Peraki Bay and along the east coast of the South Island of New Zealand may indicate the direction and speed of transport.

Banks Peninsula supports a large *H. iris* stock on a well-defined area of rocky shore with long stretches of sandy beach to the north and south. South of Banks Peninsula the closest population of *H. iris* is near Oamaru, about 190 km away, and to the north abalones occur again just north of the Waipara River, 50 km from Banks Peninsula (Fig. 2.1).

## 5.2 CIRCULATION WITHIN PERAKI BAY

### 5.2.1 Methods

A series of depth profiles of Peraki Bay were taken on 20 January 1974, using a continuously recording echo sounder.

On eight occasions during the 1973-74 summer a kilogram of rhodamine BN dye was released into the bay, and subsequent movement of the dye spot plotted. Observations of wind strength (Beaufort scale) and direction were made concurrently. On several other occasions the general pattern of surface air flow under various wind conditions within Peraki Bay was recorded by plotting the movement of wind gusts over the sea surface.

Wind directions at Christchurch airport at 0900 hours during February, March and April (the months during which *H. iris* usually spawns) from 1971 to 1974 inclusive were obtained from the Canterbury Meteorological Service. These records would not always reliably reflect the wind directions within Peraki Bay, which is subject to coastal breezes, but they indicate the general direction of surface water currents.

### 5.2.2 Results

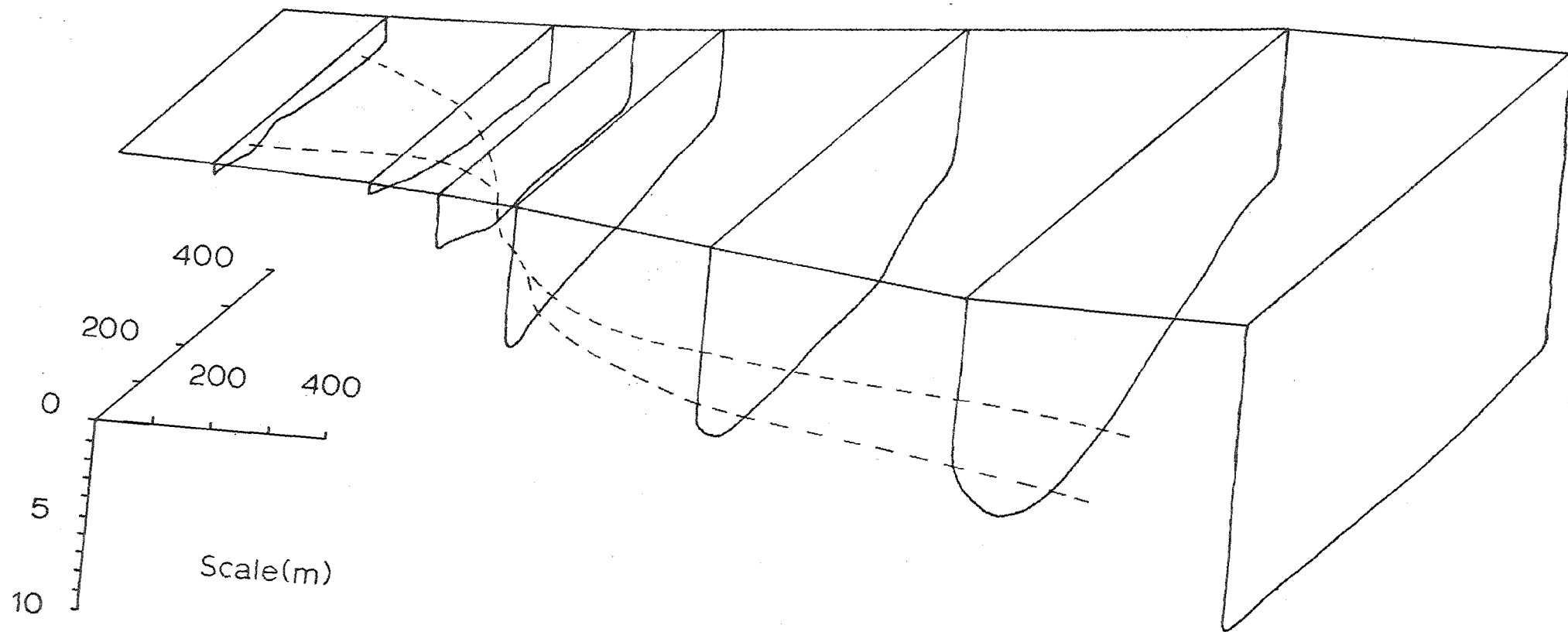
The depth profiles revealed the presence of a scour channel about 1 to 1.5 m deep and from 50 to 150 m wide across Peraki Bay (Fig. 5.1). The substrate over much of the bottom of the bay consists of fine sediment, suggesting that the major bottom current is located in this channel.

From the depth profiles, the volume of water within Peraki Bay at different stages of the tidal cycle was calculated (Table 5.1) assuming a 1.4 m and 2.1 m change in water level during neap and spring tides respectively. These values were chosen from tide tables as being typical of the region.

Table 5.1 Volume of water in Peraki Bay at various tidal states

Displacement from datum (m)	Tide	Volume ( $\times 10^6 \text{ m}^3$ )
0.2	L.W.N	10.2
1.6	H.W.N	11.9
-0.2	L.W.S	9.7
1.9	H.W.S	12.3

Figure 5.1 Bathymetry of Peraki Bay, as measured by echo sounding transects, corrected to mean water level. The dashed line marks a scour channel in the soft sediment bottom, reflecting the presence of a strong bottom current.



In terms of the change in volume, about 14% of the water within Peraki Bay at high neap tide is flushed from the bay as the tide falls. The corresponding figure for spring tides is 21%. Observations of tidal effluent on occasions when the water within the bay carried a higher silt load than the surrounding sea suggested that very little of the water flushed from Peraki Bay returned on the following tide. If the bay is assumed to be thoroughly mixed with an average loss in water volume of 17% during tidal ebb, then even if 25% of this water returns on the following tide, only about 7% of the water initially in Peraki Bay will still be present after 10 days.

The general patterns of air flow found in Peraki Bay during different wind conditions are shown in Fig. 5.2. The wind-induced surface currents would be expected to follow the same patterns with a directional displacement to the left of something less than  $20^{\circ}$  due to the coriolis effect (Lee and Ramster, 1968).

Air flow is greatly affected by the topography of Peraki Bay. Winds from the north-west through to the east are guided down by the steep-sided valley and at sea level their directions are virtually identical (Fig. 5.2b). Such winds are strongest along the eastern shore of the bay whereas the western shore is relatively sheltered. The wind patterns during south-easterlies through to south-westerlies are also very similar to one another within the bay. South-westerlies enter the bay directly and are channelled by the hills to flow almost north-south on reaching the inner shore (Fig. 5.2c). These winds lose

little of their force on entering the bay, and are particularly strong along the eastern shore. The main air flow during south-easterly winds is deflected up to an altitude of about 150 metres by the cliffs on the seaward side of the eastern headland. Surface winds sweep around the eastern point and into the bay until travelling almost north-south (Fig. 5.2d). Some air flows back toward and up the eastern shore to rejoin the higher airstream. South-easterly winds are strongest along the western shore, particularly in the seaward section, but the sea-level wind strength within Peraki Bay is far less than over the ocean just beyond.

The displacement of the rhodamine dye spots from their position of release, together with wind and tidal states, are shown in Figs 5.3 to 5.6. The length of time the dye remained visible, and the depth to which the observed movements pertain, altered with water clarity and weather conditions. In most cases the results reflect movement of the top metre of the water column.

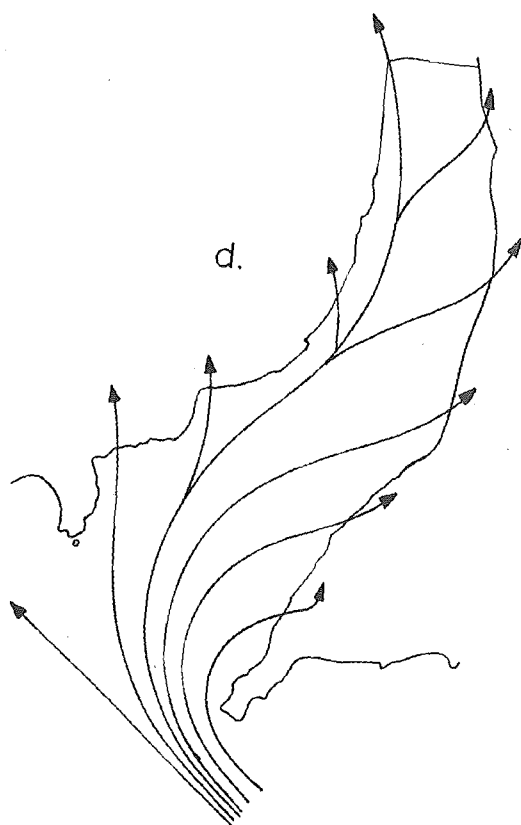
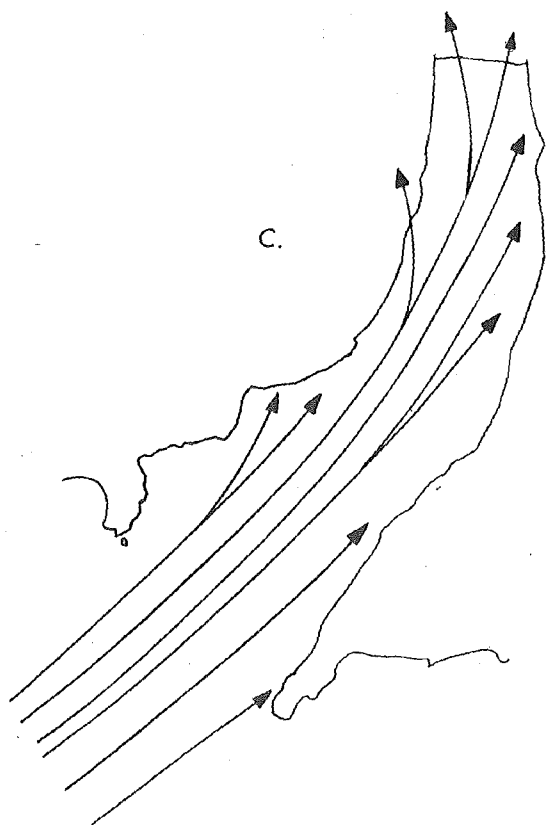
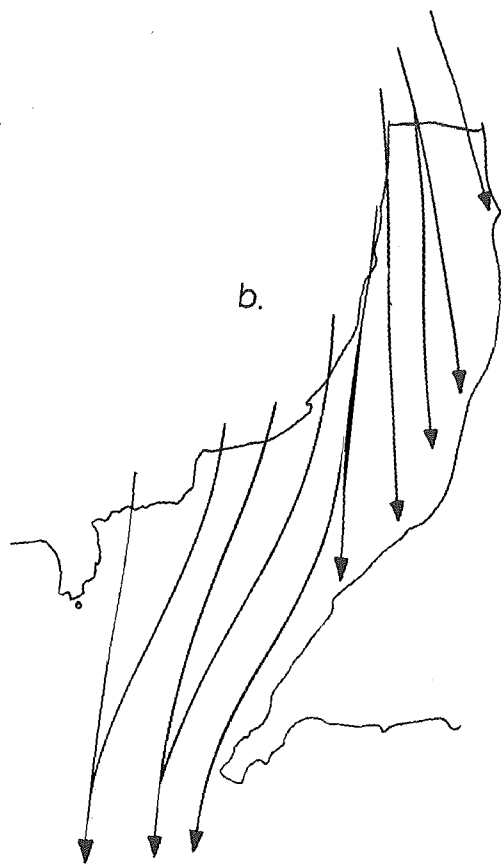
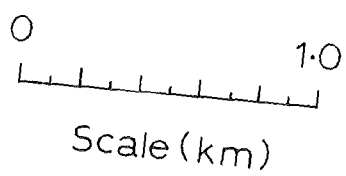
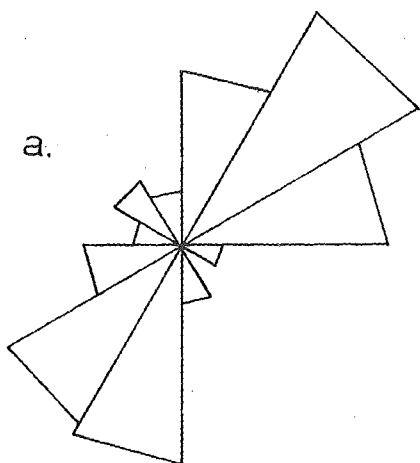
The circulation system is very variable and too few trajectories are available to quantitatively separate the influence of wind and tide on the surface waters of Peraki Bay. However, some generalizations can be made:

i) Tidal currents are weak in the north-western corner of the bay, but are very strong in the north-eastern corner.

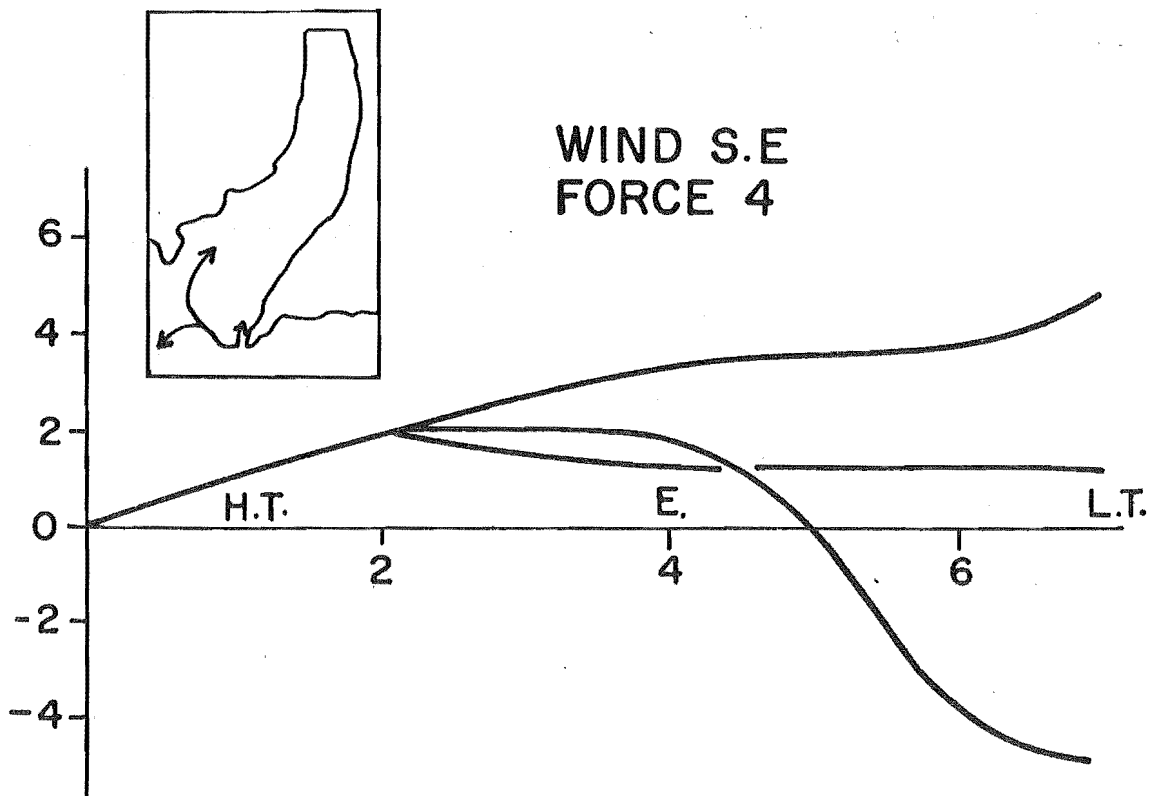
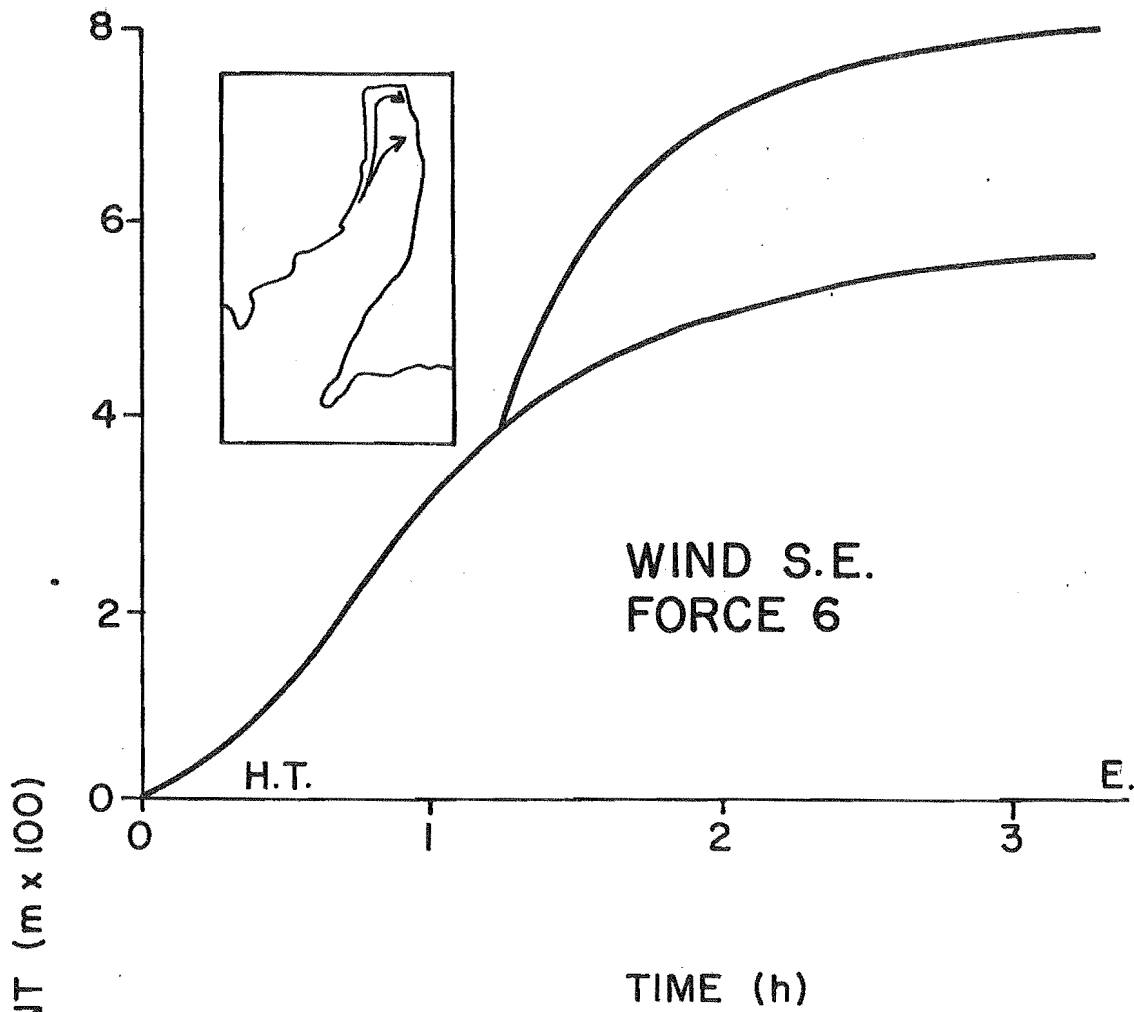
ii) movement of the surface water appears predominantly tidal for wind speeds up to force 2, whereas force 3 winds seem to approximately balance any opposed tidal flow.

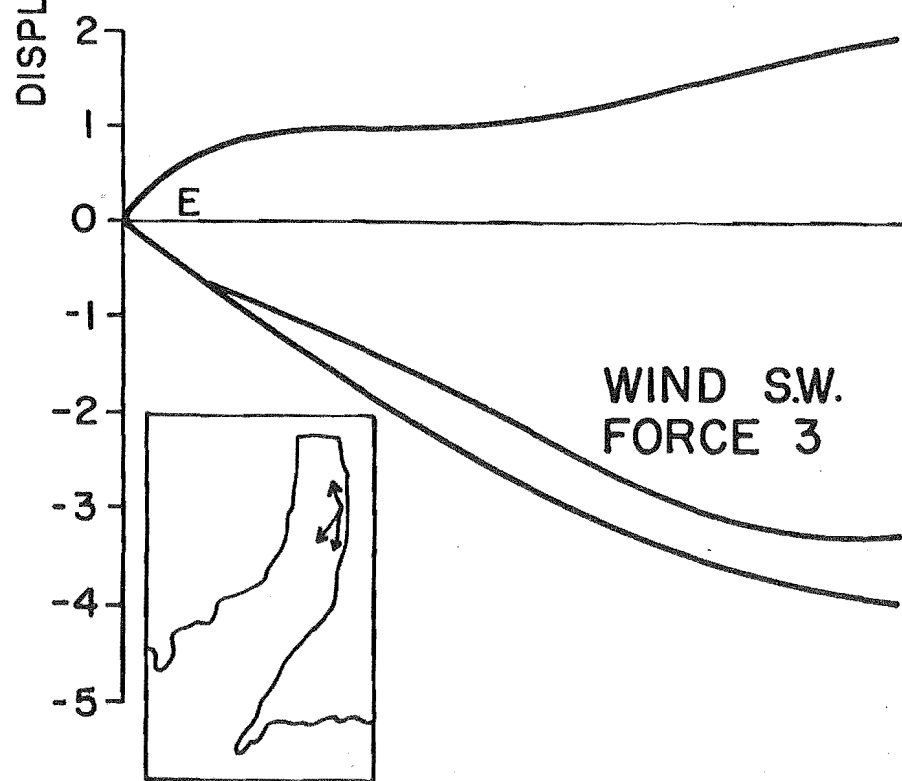
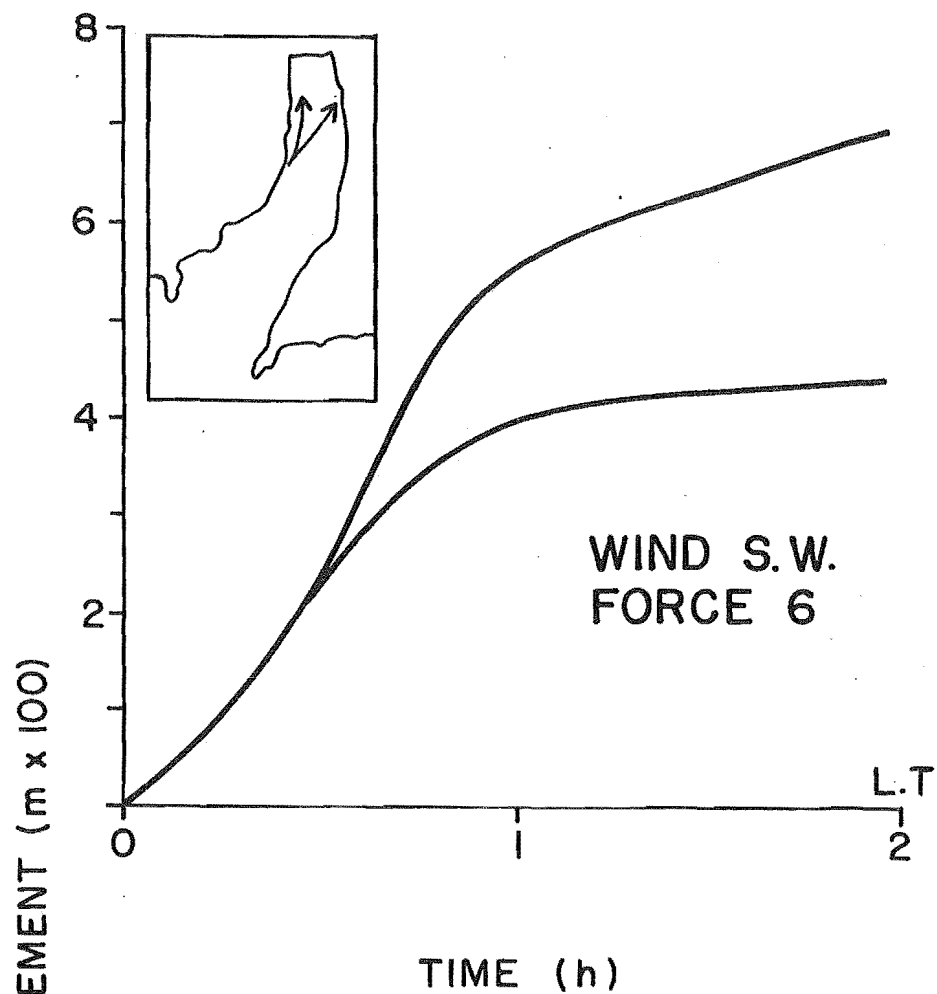


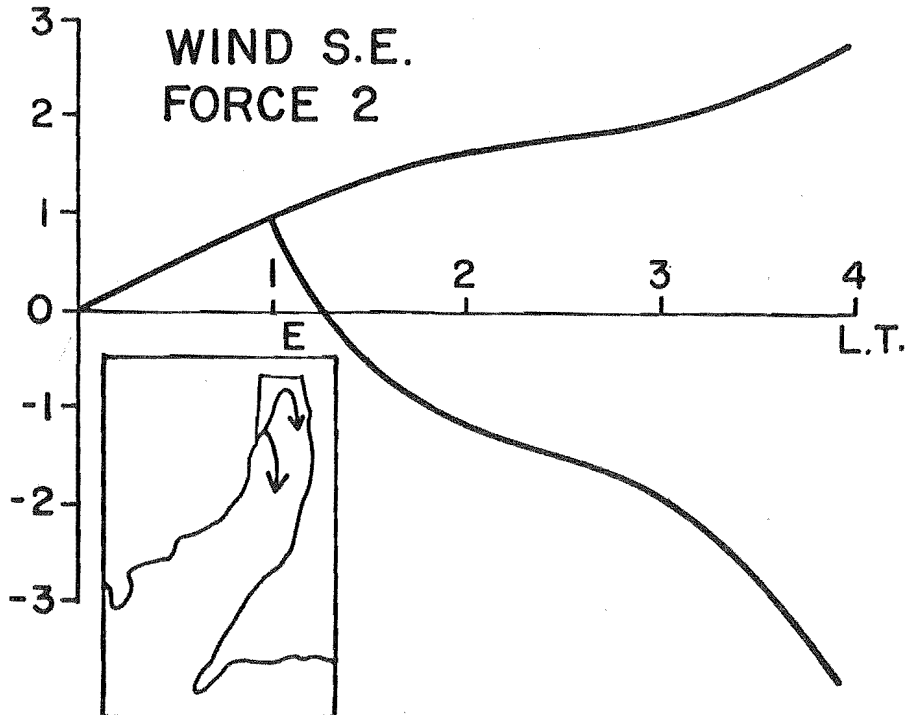
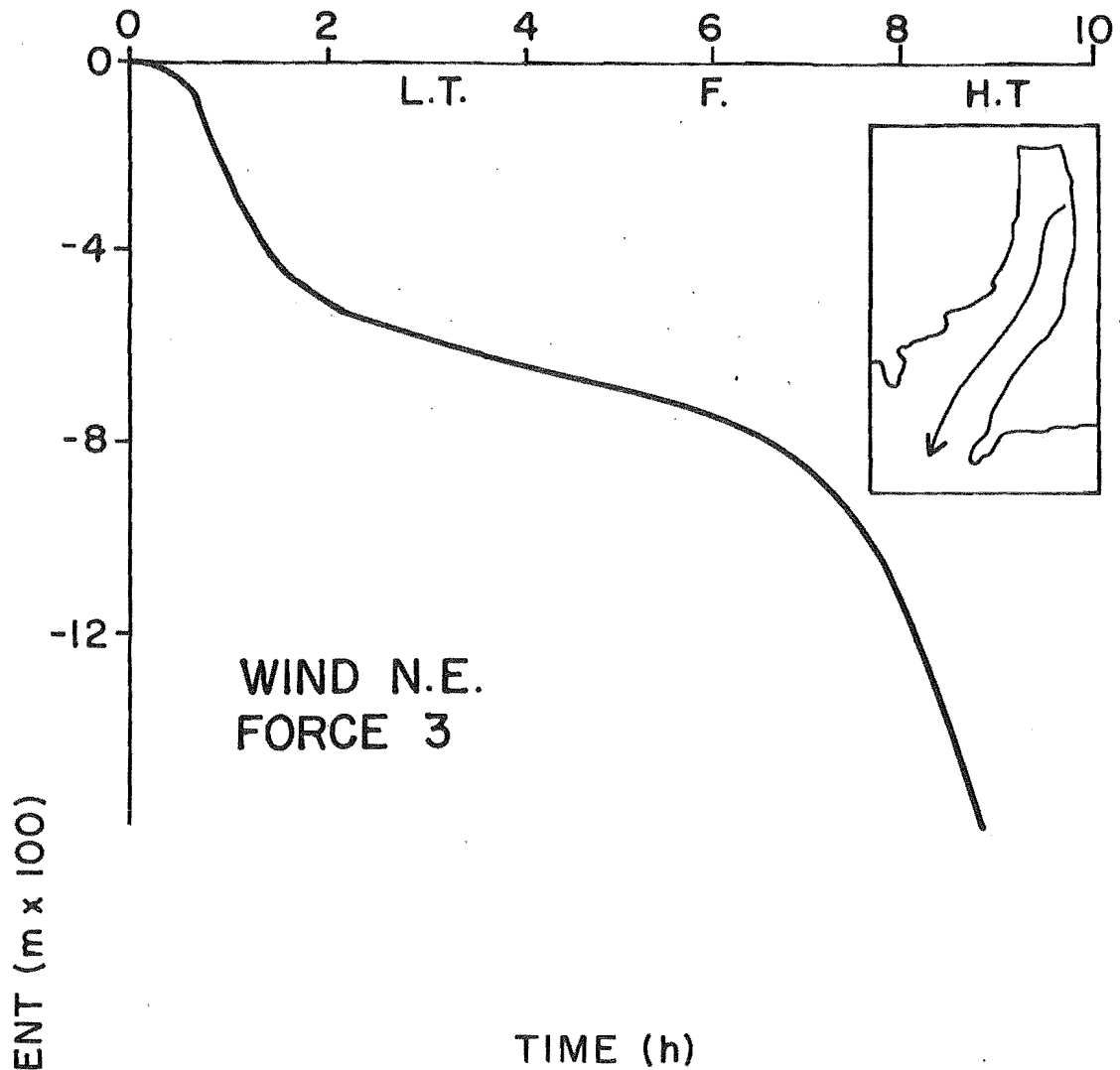
Figure 5.2 a) Wind rose based on daily wind direction at Christchurch airport at 0900 h during February, March and April 1972-1976.  
b) Wind flow at Peraki Bay during easterly-north westerly winds.  
c) As for b for south-westerly winds.  
d) As for b for south-easterly winds.

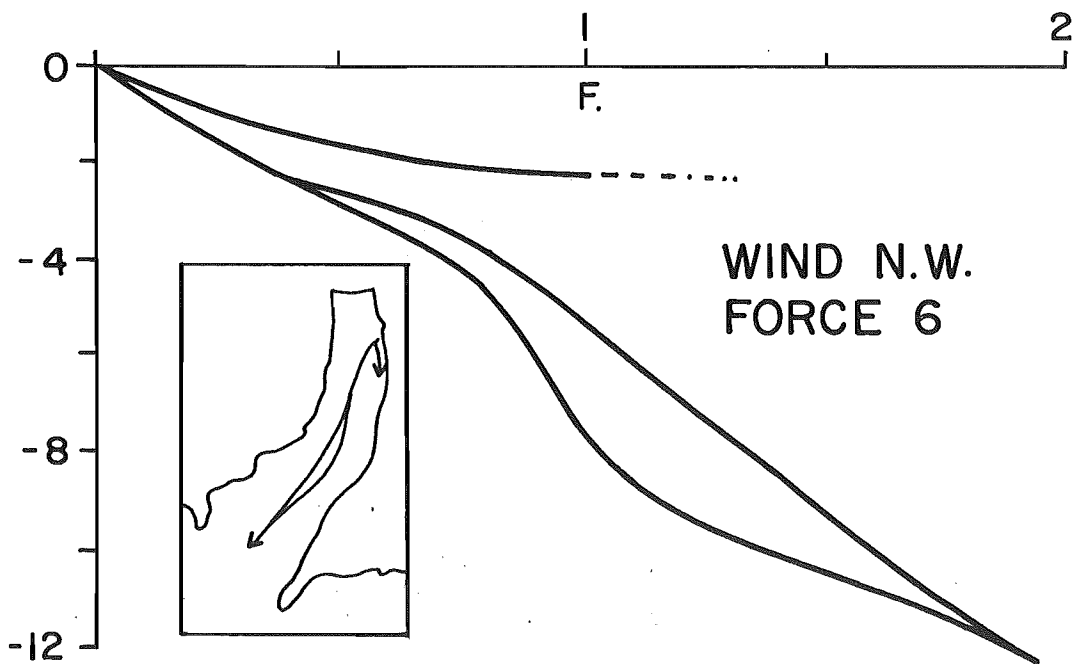
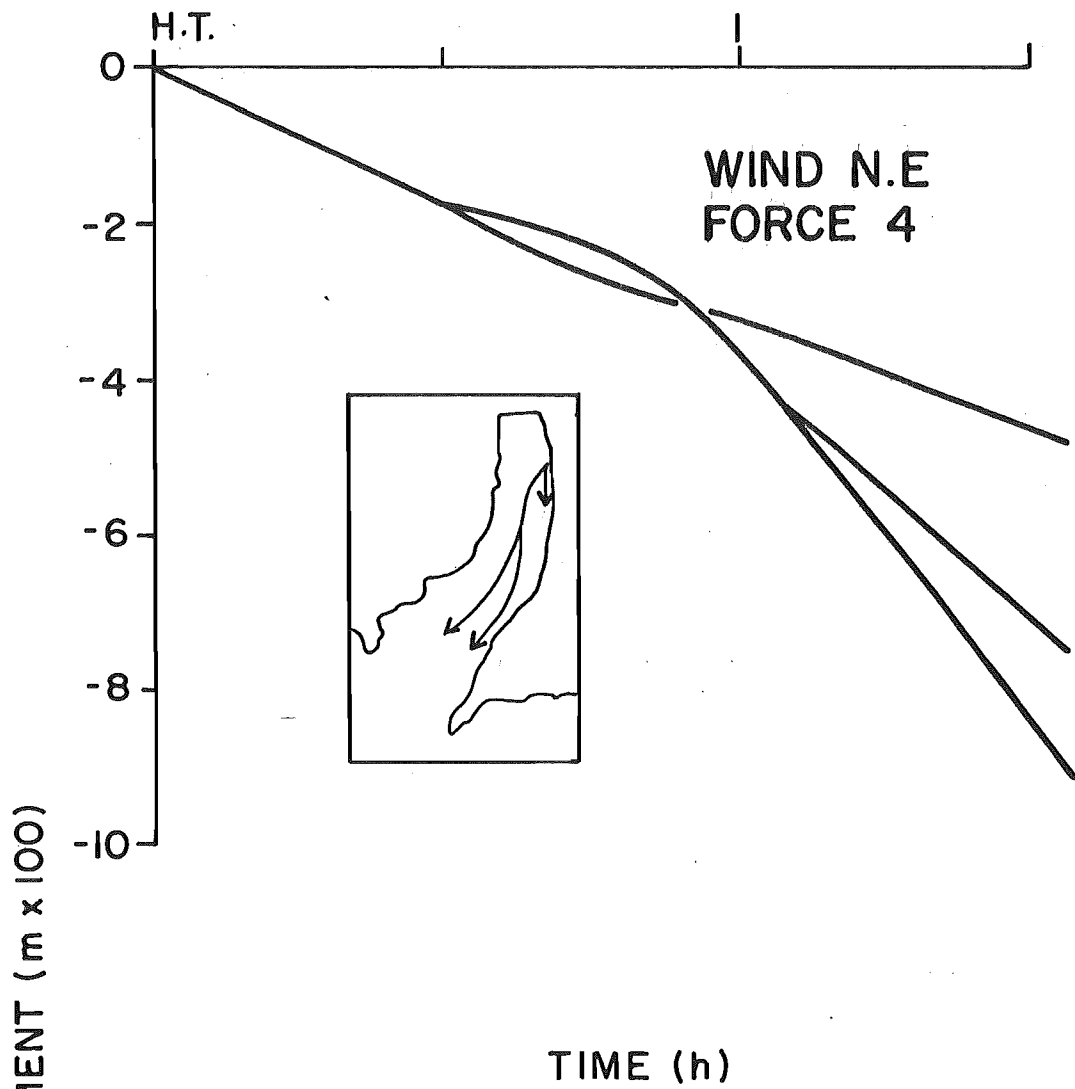


Figures 5.3 to 5.6 Displacement of rhodamine BN dye spots from their points of release in Peraki Bay. Positive displacements were to the north while negative displacements were to the south. Marked on the horizontal axis are the times of high tide (H.T.), low tide (L.T.), full flood tide (F.) and full ebb tide (E.). The inset shows the position of release within the bay and the approximate path of the dye spot(s).









Winds of force 4 or stronger drive the surface water in the same direction as the wind, irrespective of tidal flow, although a tidal component of surface current speed was occasionally apparent. Buckley and Pond (1976) found that the surface waters of a Canadian Fjord were predominantly moved by the wind and that the effects of tidal currents were negligible.

iii) There was no observable deflection of the surface water currents to the left of the wind direction, probably because Peraki Bay is shallow on an oceanographic scale and the dye was visible only to a depth of about a metre (Stevenson, 1958, in Lee and Ramster, 1968, found that the upper 15 cm of the sea moves almost parallel to the wind direction).

iv) The 'wind factor',  $k$ , is the wind-induced current speed as a percentage of the wind speed (see Lee and Ramster, 1968). Conservative values of  $k$ , calculated using the position of each dye spot at the end of each period of observation, ranged from 0.06% to 2.64%. The wind factor of 0.06% resulted from dye retained within the *Macrocystis* belt (Fig. 5.3b). The lowest measurement in open water was 0.26%. These values of  $k$  do not represent the effects of wind alone. They combine the effects of measurement error, variability in the tidal component of surface water flow, and changes in the true value of  $k$  with wind speed and sea conditions. However, in combining the second and third of these factors, the measurements provide estimates specific to Peraki Bay of the overall effect of wind on the sea surface.



Lee and Ramster (1968) considered that the actual value of  $k$  is about 2-3.5% and that it increases with wind speed.

The times taken for water to travel the length of Peraki Bay (about 2 km) under various wind strengths and with  $k$  equal to 0.05%, 0.26% and 2.6% are shown in Table 5.2.

Table 5.2 Time taken to travel the length of Peraki Bay under various wind strengths and at different values of  $k$

Wind force (Beaufort scale)	Wind speed (km/h)	Time to travel 2 km (days)		
		$k=0.05\%$	$k=0.26\%$	$k=2.6\%$
0	0.9	185	35	3.5
1	3.6	46	8.8	0.87
2	9.3	18	3.4	0.34
3	15.7	10	2.0	0.20
4	25.0	6.6	1.3	0.13
5	35.2	4.7	0.92	0.09
6	45.4	3.6	0.71	0.07
7	56.4	2.9	0.58	0.05
9	68.5	2.4	0.45	0.04
9	76.5	2.1	0.41	0.04
10	95.5	1.7	0.30	0.03

Water retained between the coast and the *Macrocystis* bed during northerly winds of up to force 4 could remain within Peraki Bay for at least 6 days. However, surface water beyond the *Macrocystis* during light (force 2) northerly winds would be transported from the bay within about three days. One day of force 4-5 northerly wind would probably transport most of the surface water out of Peraki Bay.

### 5.3 CIRCULATION ON THE EAST COAST OF THE SOUTH ISLAND

The ocean currents in this region have been described by Brodie (1960), Burling (1961), Jillet (1969) and Heath (1972b). Heath's description is summarized in Fig. 5.7.

The geostrophic velocity of the Southland current off the Otago Peninsula was calculated by Heath (1972b) to be  $0.07$  to  $0.08 \text{ ms}^{-1}$  directed to the north. A single drogue released in the region and stationed at a depth of  $50 \text{ m}$  during strong north-easterly winds (Heath, 1973), moved to the south with a speed of  $0.23 \text{ ms}^{-1}$ , indicating that the general northerly flow may be reversed under some conditions.

The velocity of the surface current between Otago Peninsula and Banks Peninsula was measured directly by Heath (1973). The direction of flow was variable, and current speeds ranged from  $0.20$  to  $0.90 \text{ ms}^{-1}$ . Surface water movement in this region has also been investigated using drift cards and bottles. At fortnightly intervals between 1920 and 1922, drift bottles were released from the Otago Peninsula (Thomson, 1922, in Brodie, 1960). Drift direction was variable near the point of release but otherwise transport was to the north. Of five hundred drift cards released from the Otago Peninsula by Robertson (1973) 58 were recovered, and of these 56 had travelled north. Those which reached the Canterbury coast travelled with an average minimum speed of  $0.15 \text{ ms}^{-1}$ . Drift card speeds obtained by R. Herzer (Victoria University of Wellington, pers. comm.), from releases in the vicinity of Banks Peninsula, were lower than those reported by Robertson but still showed a clear northward movement (Fig. 5.8).

Figure 5.7 Generalised ocean current system along the  
east coast of the South Island of New Zealand  
(after Heath, 1972b).

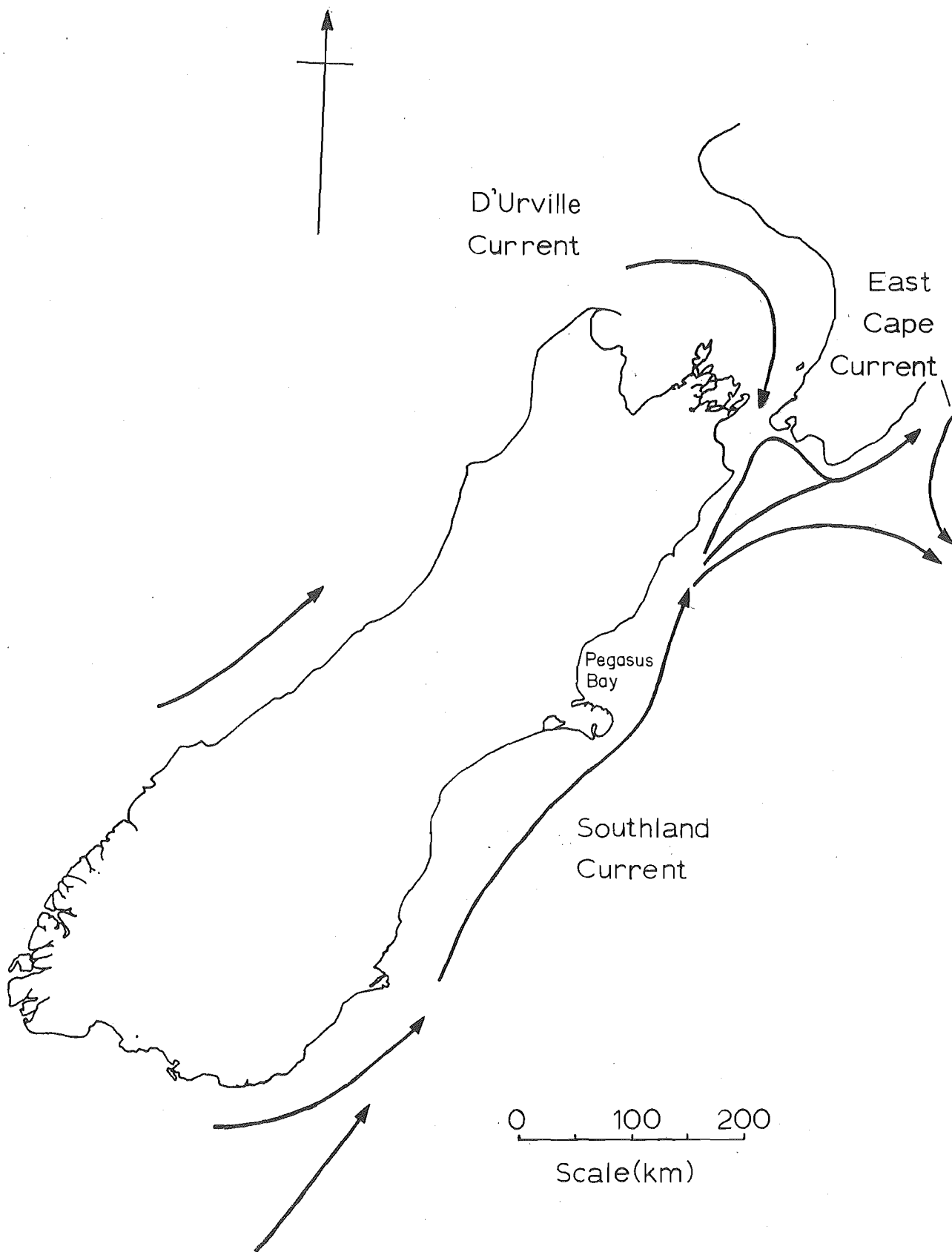
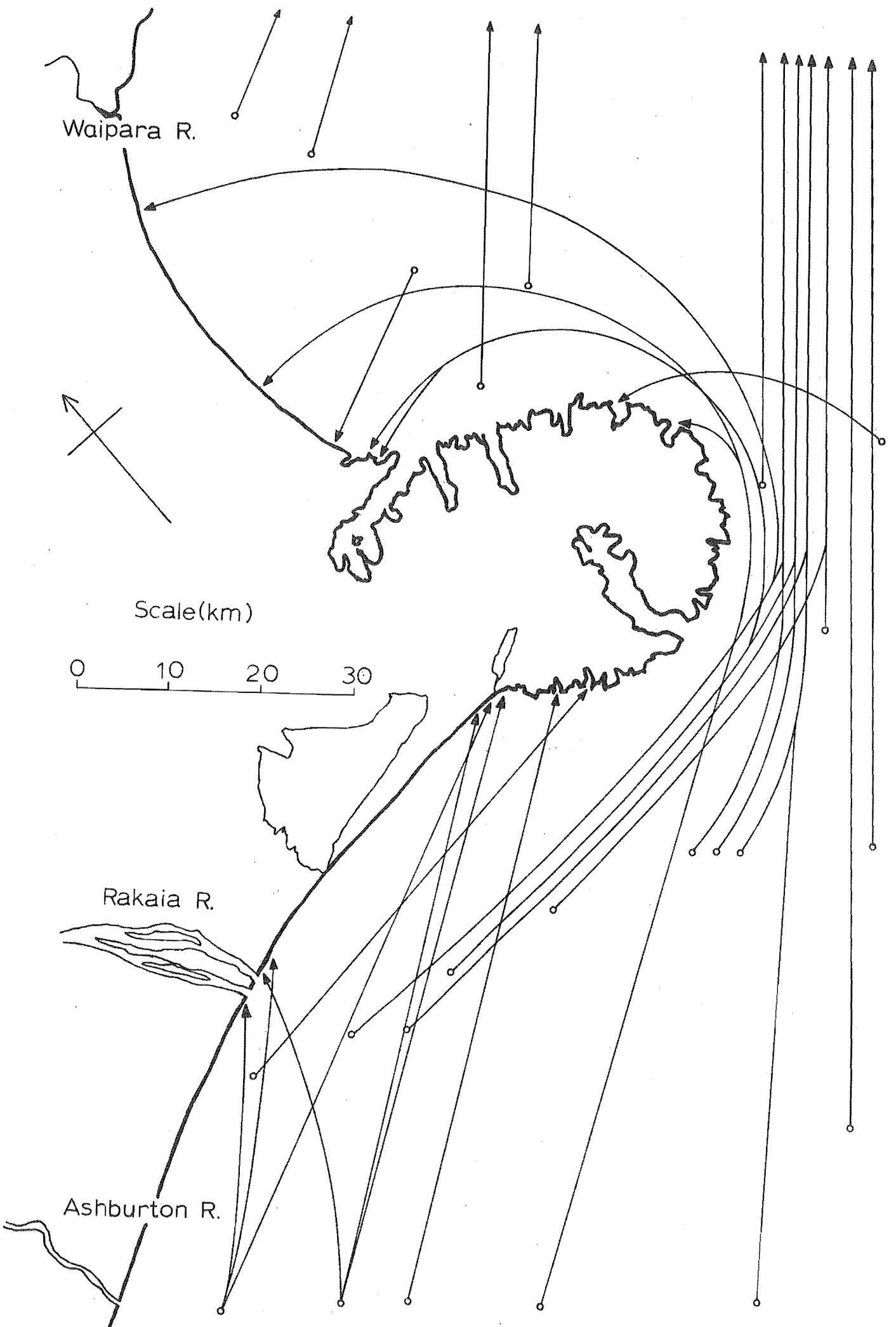


Figure 5.8 The most direct trajectories of returned drift cards released by R. Herzer (Victoria University of Wellington, pers. comm.) in the vicinity of Banks Peninsula.



Cards released south of Banks Peninsula moved north in spite of adverse winds. The average minimum surface speed, calculated on the basis of the trajectories shown in Fig. 5.8, was  $0.07 \text{ ms}^{-1}$ . The highest speed for a card recovered in Canterbury was  $0.13 \text{ ms}^{-1}$ .

From drogue trajectories, Heath (1973) found that the speed of the Southland current just north of Banks Peninsula was  $0.26 \text{ ms}^{-1}$  and  $0.08 \text{ ms}^{-1}$  at depths of 100 mm and 300 mm respectively. The current direction was generally to the north, but tidal influence in the region was strong and capable of reversing flow. Direct measurements of the surface currents just north of Banks Peninsula, made in April 1971 during very strong northeasterly winds, gave current speeds from  $0.1 \text{ ms}^{-1}$  to  $0.8 \text{ ms}^{-1}$ , generally in the direction of the wind (Heath, 1973). Earlier calculations (Heath, 1972a) from wind speed records taken at the same time of the year suggested surface current speeds of  $0.01$  to  $0.09 \text{ ms}^{-1}$  in this area.

Dawson (1954) made an extensive drift card study in Pegasus Bay. He found that the surface circulation was predominantly wind driven, but even during periods of northeasterly winds, cards released north of Motunau (25 km north of the Waipara River) did not travel south into Pegasus Bay. Of the 450 bottles and 900 cards released throughout Pegasus Bay under a variety of wind conditions, only one reached the northern coast of Banks Peninsula, and none was found to have travelled to its eastern or southern coasts. This is in strong contrast to the results obtained by Herzer for cards released adjacent to, and south of, Banks Peninsula.

#### 5.4 DISCUSSION

What little is known concerning the larval behaviour of *H. iris* suggests that the larvae maintain station in the surface waters and thus it is unlikely they could remain in Peraki Bay for the duration of larval life. Besides the considerable flushing action of the tides, most larvae in the upper metre of the water column during force 3 or stronger easterly to north-westerly winds would be removed within a day or two. Such winds occurred on about half of the February, March and April days (when abalone usually spawn) between 1972 and 1975.

Once in the surrounding coastal waters the larvae would generally be taken north, where they could provide recruitment to other bays on Banks Peninsula and to populations north of the Waipara River. It appears that larvae which are planktonic for 8-10 days could reach Kaikoura, but since suitable settlement habitat is available over a large proportion of this journey the planktonic phase may not extend for the full period possible. Thus the bulk of larvae produced on Banks Peninsula probably settle between the Waipara River and Kaikoura.

Still assuming that larval *H. iris* travel in the surface waters, Banks Peninsula is most likely to receive its recruitment from the south. To travel the 190 km from coastal Oamaru to Banks Peninsula in 10 days would require an average speed of about  $0.22 \text{ ms}^{-1}$ . The hydrological data available suggest that this is possible.

The recruitment patterns at Peraki Bay and Kaikoura (Chapter 4) are also consistent with the hypothesis that



the bulk of a population's recruitment is not produced by local adults.

If the general trends for larval dispersal deduced from current patterns are realistic, one would expect the recruitment to Peraki Bay to be more variable than that to Kaikoura. Transport of larvae to Peraki Bay from coastal Oamaru would require persistent favourable winds (southerlies-westerlies) which could not be expected to occur every year. Recruitment to Peraki Bay during spawning seasons dominated by northerly winds would probably be low, because they would transport locally-produced larvae to the south. Larvae moving southward, during northerly winds, on to Banks Peninsula from stocks further north could provide recruitment to the northern and eastern shores of the Peninsula, but they are unlikely to travel against the off-shore surface currents and reach the southern coast. In contrast, Kaikoura would probably receive good recruitment under a wide variety of wind conditions because abalones are common along most of the coastline within 100 km to both the north and south, and the Kaikoura Peninsula is unlikely to modify the current pattern to the same extent as the much larger Banks Peninsula.

The information available is not sufficient to conclude that transport of larval *Haliotis iris* over distances of 50 to 200 km is a regular feature in the population dynamics of the species, despite the theoretical possibilities. Other explanations, including a highly variable and/or density-dependent larval mortality, could

equally account for the observed recruitment patterns without requiring a significant proportion of the larvae produced by a population to be transported over large distances. Also, the dense *Macrocystis pyrifera* forest in Peraki Bay may play an important role in limiting dispersal of larvae by acting as a partial barrier to movement of water adjacent to the coast into the bay at large.

Clarification of the situation would be greatly aided by the following work:

i) A more detailed examination of larval behaviour, particularly under field conditions. This was attempted during March and April 1974 and 1975, when plankton samples were taken off the coast of Banks Peninsula. The few species of gastropod veliger present at this time of the year were predominantly in the surface metre of the water column, but the larval stages of *H. iris* could not be identified with certainty.

ii) Continued surveillance of the Oamaru, Banks Peninsula and Kaikoura spawning and recruitment patterns. This could eventually allow the degree of correlation between spawning and recruitment in the different localities to be established.

iii) The monitoring of recruitment to an isolated population such as that on the Chatham Islands. If larvae cannot remain localized to any extent, it would be expected that such a population would receive strong recruitment from the mainland during spawning seasons dominated by winds favourable to larval transport from the South Island of New Zealand, with low 'residual' recruitment

from the local population and 'strays' from the mainland during intervening years. However, a reasonably constant recruitment to the Chatham Island population is unlikely to result from surface transport over the 600 km distance from the mainland since it is unlikely that favourable weather conditions would occur every year.

## 6. MORTALITY AND ITS CAUSES

### 6.1 MORTALITY

#### 6.1.1 Introduction

Very little is known about the pattern and level of mortality in haliotids, nor of the related topic, longevity. However, the slow growth rate and large maximum size reported for many haliotid species suggest that they are generally long-lived.

The mortality rate of a marine species is usually estimated by the analysis of age structures or from the results of large scale tagging programmes. Because haliotids generally cannot be aged over most of their life span the analysis of their age structures is impossible, and until recently (Beinssen and Powell, 1976) the difficulty of tagging and recovering large numbers of abalone precluded the estimation of mortality from tag return data. The study by Beinssen and Powell was part of a large and well supported investigation into the Australian abalone fishery, and involved the tagging of about 1875 animals.

The mortality of *H. iris* at Peraki Bay was estimated from a knowledge of individual growth rates and population size structure. Because Peraki Bay has been subject to negligible fishing pressure, all estimates of the total mortality ( $Z$ ) may be taken to be estimates of the natural mortality ( $M$ ).

### 6.1.2 Methods

Mortality could not be estimated from the results of tagging experiments because the tagged group (see Chapter 3) could not be visited often enough to distinguish between the possible fates of apparently absent tagged animals, i.e. dead, lost tag, emigrated, or present but concealed. The mortality was therefore estimated by four indirect methods. The first method utilised estimates of the recruitment and number of animals in the population, and methods two, three and four used the population length frequency structure and individual growth rates.

The methods used were:

Method i): If a population of  $N$  individuals (just after recruitment) is stable with a constant annual recruitment and mortality rate, then the recruitment equals the number of animals dying each year. Thus:

$$R = N(1 - e^{-Z})$$

where  $R$  is the annual recruitment and  $Z$  is the annual instantaneous mortality (see Ricker, 1958). From which

$$Z = \ln \left( \frac{N}{N - R} \right)$$

$Z$  was calculated from the estimates of the total population and recruitment of two year olds in February 1976 (see Chapters 2 and 4). The mortality given by this method must be regarded as approximate as it is very sensitive to violation of the assumption of constant recruitment. The recruitment in 1976 may have been lower than that necessary to maintain the stock at the current level (Chapter 4) and

so this method may underestimate mortality.

Method ii): Beverton and Holt (1956) derive the equation

$$Z = \frac{K (L_{\infty} - \bar{L})}{(\bar{L} - l_c)}$$

where  $Z$  is the annual instantaneous mortality,  $k$  and  $L_{\infty}$  are the parameters of Von Bertalanffy growth,  $\bar{L}$  is the mean length of animals in a sample and  $l_c$  is the mean length at recruitment. The derivation assumes that mortality and recruitment are constant, that the population has a stable structure, and that the growth of all individuals is described by the Von Bertalanffy equation.

This method was applied to the total population structure data collected in February 1976 and to the size structure of animals in the EI stratum in February 1974, February 1976 and December 1976. The parameter values used were  $K = 0.171$ ,  $L_{\infty} = 130.0$  mm and  $l_c = 30$  mm (Chapter 2).

Method iii): Ssentongo and Larkin (1973) show that

$$Z = \frac{n}{n+1} \cdot \frac{K}{\ln(1 - \frac{l_c}{L_{\infty}}) - \ln(1 - \frac{\bar{L}}{L_{\infty}})}$$

where  $n$  is the sample size and the other symbols are the same as in method (ii) above. It is assumed that recruitment and mortality are constant, that the population has a stable structure and that all individuals grow as predicted by the Von Bertalanffy equation.

This method was applied to the total population structure data collected in February 1976 and to the size

structure of animals in the EI stratum in February 1974, February 1976 and December 1976. The parameter values used were  $K = 0.171$ ,  $L = 130.0$  mm, and  $lc = 30$  mm (Chapter 3).

Method iv): The population model described in Chapter 1 provides  $i$  equations predicting the number of animals in each of  $i$  size classes at time  $T+t$  ( $\hat{\eta}_{j,T+t}$ ;  $1 \leq j \leq i$ ) given the number present at time  $T$  ( $\eta_{j,T}$ ). For non-negative growth the equation set is

$$\begin{aligned}\hat{\eta}_{1,T+t} &= R_1 + S_{1,1} P_{1,1} \eta_{1,T} \\ \hat{\eta}_{2,T+t} &= R_2 + S_{2,1} P_{2,1} \eta_{1,T} + S_{2,2} P_{2,2} \eta_{2,T} \\ &\vdots \\ \hat{\eta}_{i,T+t} &= R_i + \sum_{k=1}^{k=i} S_{i,k} P_{i,k} \eta_{k,T}\end{aligned}\tag{1}$$

As described in Chapter 1,  $P_{i,k}$  is the proportion of the animals in size class  $k$  at time  $T$  which will grow to be in size class  $i$  at time  $T+t$ ,  $S_{i,k}$  is the survival of these animals and  $R_i$  is the recruitment (assumed to occur at the end of time interval  $t$ ) to size class  $i$ . If necessary the  $R_i$  may be treated as the elements of a 'net migration' vector and combine the effects of emigration, immigration and the recruitment of young animals.

Equation (1) may be used to calculate size specific survival. If  $S_{j,k}$  is replaced by  $S_j$  for all  $k$  (i.e. the survival of animals reaching size class  $j$  at time  $T+t$  was the same no matter what size class they were in at the beginning of the time interval), then

$$S_j = \frac{\eta_{j,T+t} - R_j}{\sum_{k=1}^j P_{j,k} \eta_{k,T}} \quad (2)$$

Since the mean and variance of  $\eta_{j,T+t}$  and  $\eta_{j,T}$  are known from analysis of data collected during a sampling programme, an approximate confidence region may be obtained for the survival estimates by repeated solution of the equation using values of  $\eta_{j,T}$  and  $\eta_{j,T+t}$  which are randomly chosen from their respective distributions.

The population structure data from Peraki Bay were not sufficiently precise to allow application of equation (2). The large variances associated with the population structures produce a very wide range of possible survival values for each size class.

By assuming survival is not size specific, equation (1) may be used to provide a least squares estimate of the overall survival  $S$ , i.e.  $S_{j,k} = S$  for all  $j$  and  $k$ . The quantity  $(\hat{\eta}_{j,T+t} - \eta_{j,T+t})^2$  may be considered a least squares difference, and so

$$\begin{aligned} L &= \sum_{j=1}^{j=i} (\hat{\eta}_{j,T+t} - \eta_{j,T+t})^2 \\ &= \sum_{j=1}^{j=i} \left[ R_j + S \left( \sum_{k=1}^{k=j} P_{j,k} \eta_{k,T} \right) - \eta_{j,T+t} \right]^2 \end{aligned}$$

Setting the derivative of  $L$  with respect to  $S$  equal to zero gives

$$\sum_{j=1}^{j=i} R_j \sum_{k=1}^{k=j} P_{j,k} \eta_{k,T} + S \sum_{j=1}^{j=i} \left( \sum_{k=1}^{k=j} P_{j,k} \eta_{k,T} \right)^2 - \sum_{j=1}^{j=i} \eta_{j,T+t} \sum_{k=1}^{k=j} P_{j,k} \eta_{k,T} = 0$$



and the least squares estimate of  $S$  is

$$S = \frac{\sum_{j=1}^{j=i} \eta_{j,T+t} \sum_{R=1}^{k=j} P_{j,k} \eta_{k,T} - \sum_{j=1}^{j=i} R_j \sum_{k=1}^{k=j} P_{j,k} \eta_{k,T}}{\sum_{j=1}^{j=i} \left( \sum_{k=1}^{k=j} P_{j,k} \eta_{k,T} \right)^2} \quad (3)$$

The instantaneous mortality rate is then given by  $-(\ln S)/t$  and an approximate confidence interval for  $S$  may be found as for the estimates of size specific survival from a knowledge of the variances of  $\eta_{j,T}$  and  $\eta_{j,T+t}$ .

More complex equations result if there is a need to consider recruitment to have occurred more than once or at some time between  $T$  and  $T+t$  (for example, if recruitment occurs annually and the population structure is known just after recruitment in one year and just after recruitment two years later). Sets of equations analogous to equation (1) may be derived for such situations and solved using a generalized non-linear least squares algorithm such as the Marquardt algorithm (Conway, Glass and Wilcox, 1970).

Equation (3) was applied to the Peraki Bay data in two ways:

Method i va): Assuming the population has a stable structure, then  $\eta_{j,T+t} = \eta_{j,T}$  when the interval  $t$  is about one year. Under this assumption, survival was calculated using equation (3) from the total population size structure in February 1976 and from the size structure of animals in the EI stratum in February 1974, February 1976 and December 1976.

Method ivb: Two estimates of survival were obtained by applying the logic of equation (3) (i.e. not assuming stability) to the size structure data from the EI stratum. One estimate relates to the period from February 1974 to February 1976 (using a more complex form of equation (3) which was solved using the Marquardt algorithm), and the other to February 1976 to December 1976 (using equation (3) as written). These estimates assume there was no net migration across the borders of the stratum, which is probably reasonable.

The growth parameters used for methods iva and b were  $K = 0.1636$ ,  $L_{\infty} = 131.9$  mm,  $\sigma_K^2 = 0.0118$  and  $\sigma_{L_{\infty}}^2 = 138.7$  mm (see Chapter 3).

Recruitment of two year olds was considered to occur in early February each year, and the estimates given in Chapter 4 were used. Recruitment to the EI stratum in 1975 was assumed to be 2500. Both methods iva and b are insensitive to variability in the recruitment estimates over the time intervals used. (A 10% change in the recruitment results in a less than 1% change in the estimated survival.)

Approximate confidence intervals were obtained for the survival estimates provided by each method by utilising the known variability of the parameters: population size and recruitment for method i;  $L_{\infty}$  and  $K$  for methods ii and iii; population structure,  $L_{\infty}$ ,  $K$ ,  $\sigma_{L_{\infty}}^2$ ,  $\sigma_K^2$ , and recruitment for methods iva and ivb. Each method was repeatedly solved (100 times for methods i, ii and iii, and 250 times for methods iva and ivb) with the parameters chosen randomly from a normal distribution with the

appropriate mean and variance. The 90% confidence interval was then obtained such that 5% of the solutions were in each tail of the distribution of solutions (survival was taken to be bounded 'naturally' at the value 1.0). The distributions of the growth parameter estimates for methods iva and ivb are not normal, but because these methods appear to be critically dependent on the estimates of population structure rather than growth or recruitment, very little error will result from their being treated as normal random variates.

#### 6.1.3 Results

The mortality estimates are shown in Table 6.1. The mean values of the estimates differ between methods, but the confidence regions of the estimates provided by methods ii, iii and iv are all very similar. The estimates derived by method i suggest that the annual survival is greater than 0.93, but in view of the low recruitment to Peraki Bay during the period covered by the study (see Chapter 5), method i almost certainly overestimates survival.

Within each of the methods there is a progressive decrease with time of the mortality estimated for animals in the EI stratum. For methods i through iva this is probably because the years of poor recruitment slowly skewed the length frequency distribution to the left (see Fig. 2.6), causing a progressive departure from the size structure expected under stable conditions and an increase in average length. Under the assumption of stability this increase in mean length was reflected as a decrease in mortality.

Table 6.1 Annual survival (S) and instantaneous natural mortality (M) of *H. iris* at Peraki Bay. The approximate 90% confidence interval for survival is given in brackets below each estimate of survival. Methods i through iva assume a stable population structure whereas method ivb does not. All estimates relating to the EI stratum assume there to be no net migration across the boundaries of the stratum.

	EI stratum Feb. 1974	Samples EI stratum Feb. 1976	EI stratum Dec. 1976	Total population Feb. 1976
Mean length (mm)	95.7	103.8	104.3	106.2
n	328	151	193	721
Method i	M 0.069 S 0.933 (0.90-0.971)	0.057 0.945 (0.909-0.971)	0.035 0.965 (0.919-0.996)	0.010 0.990 (0.971-0.997)
Method ii	M 0.089 S 0.915 (0.845-0.964)	0.060 0.941 (0.884-0.978)	0.059 0.943 (0.887-0.979)	0.053 0.948 (0.895-0.982)
Method iii	M 0.159 S 0.853 (0.760-0.926)	0.127 0.881 (0.799-0.943)	0.125 0.882 (0.801-0.944)	0.118 0.888 (0.809-0.948)
Method iva	M 0.060 S 0.941 (0.873-0.982)	0.046 0.955 (0.875-0.995)	0.035 0.965 (0.891-0.995)	0.056 0.945 (0.875-0.981)
Method ivb	M 0.089 S 0.915 (0.80-1.00)	0.065 0.938 (0.72-1.00)		

The survival estimates using method iva, which assumes stability, were higher than those provided by method ivb which does not assume stability, but the difference was not great. Thus it would appear that the assumption of a stable population structure is reasonable over a period of up to two years. This result indicates only that the population is slow to change (i.e.  $\eta_{i,T+2} \approx \eta_{i,T}$ ), due to low growth and mortality rates, and does not imply that the population is stable in the long-term, classical sense assumed by methods i, ii and iii, i.e. that the population parameters have remained constant with respect to time at least since the time of entry into the population of the oldest animal currently alive.

#### 6.1.4 Discussion

The estimates of mortality obtained using the population model presented in Chapter 2 generally agree with those of other methods, and suggest that the annual instantaneous mortality rate of *H. iris* over two years of age at Peraki Bay is between 0.05 and 0.2, and is probably about 0.1. This implies that the average age of the post-recruitment population is about 11.5 years (under steady state conditions) and that about 5% of the recruitment in any year will live to be more than thirty-two years of age. These conclusions are consistent with what little is known of the mortality and longevity of other haliotid species.

Curtner (1917) identified annual rings in *H. rufescens* and concluded that some individuals live at least thirteen years. This estimate has been quoted by Bonnet (1940), Comfort (1957) and Poore (1972c), but Cox (1962) found that

growth in *H. rufescens* was not as regular as Curtner had assumed and that growth rings did not provide a reliable estimate of age. Cox did not offer an alternative estimate of longevity. From the analysis of growth rates it appears that a South African abalone, *H. midae*, lives at least fourteen years and some individuals may be in excess of thirty years of age (Newman, 1968). Olsen (1971) estimated the weight specific natural mortality rate of *H. fulgens* from physiological data and using the equations derived by Ursin (1967). Olsen's estimates were:

Weight (g)	Annual instantaneous mortality
1	1.0
10	0.26
100	0.07
1000	0.02

He also reported that a number of *H. fulgens* introduced to the Hawaiian Islands from California survived for at least ten years (although they apparently did not breed). Smith (1972) estimated the mortality rate of *H. cracherodii* and *H. rufescens* from the population size structure and individual growth rates. He estimated the total instantaneous mortality of a heavily exploited *H. cracherodii* population to be 1.0, and that of an unexploited population of *H. rufescens* to be 0.05. These estimates must be interpreted with caution since it is doubtful whether the size structures he used were representative of whole populations, and further, the derivation of the method he employed to calculate mortality is unclear. The annual mortality rate of *H. ruber* in Australia has been estimated from the results of large tagging programmes (see Harrison

and Grant, 1971). The estimated mortality of *H. ruber* in Tasmania is 0.2 (C. Sumner, Department of Agriculture, Tasmania; pers. comm.) while the mortality of animals over three years of age on the Victorian coast ranged from 0.24 to 0.37 during four successive years (S.A. Shepherd, Department of Agriculture and Fisheries, Adelaide; pers. comm). Beinssen and Powell (1976) found that the instantaneous natural mortality of *H. ruber* from Victoria was 0.2, and considered that their estimate may have been slightly too high.

The age- or size-specific pattern of mortality in haliotids is unknown, although Comfort (1957) suggests that long-lived species of molluscs are subject to a high mortality rate as juveniles, followed by a long period of uniform, low mortality. He cites the examples of *Amphidesma ventricosum* (which lives for 6-10 years) and *Chiton tuberculatus* (which lives for about 13 years). This pattern of mortality has also been found in *Nucella lapillus* (longevity about 6 years; Feare, 1970) and *Dicathais orbita* (longevity about 19 years; Phillips and Campbell, 1974). However, Fotheringham (1971) found that mortality increased with size in *Shaskyus festivus* and *Ocenebra poulsoni* (longevity of about 10 and 9 years respectively).

## 6.2 CAUSES OF DEATH

### 6.2.1 Introduction

Haliotids are subject to a variety of physical and biological hazards. Some of the causes of death of abalones in California, Australia and New Zealand are

documented by Cox (1962), Shepherd (1973a) and Poore (1969) respectively. The main predators are crabs, starfish and fish (including rays), although a variety of other animals are known to have attacked abalone. (Crofts, 1929, reports the case of an American prairie wolf being killed when the abalone (*H. cracherodii*) it tried to eat clamped down on its nose.)

Both Cox (1962) and Poore (1969) noted that nacre blisters may be present on the inner surface of the shell and stated that they are produced by the abalone when boring organisms (in *H. iris* the polychaete *Polydora monilaris* and the barnacle *Cryptophialus melampygos*) break through the shell.

Various observations on the causes of mortality of *H. iris* at Peraki Bay were made, and the association between nacre blisters and death was examined.

#### 6.2.2 Methods

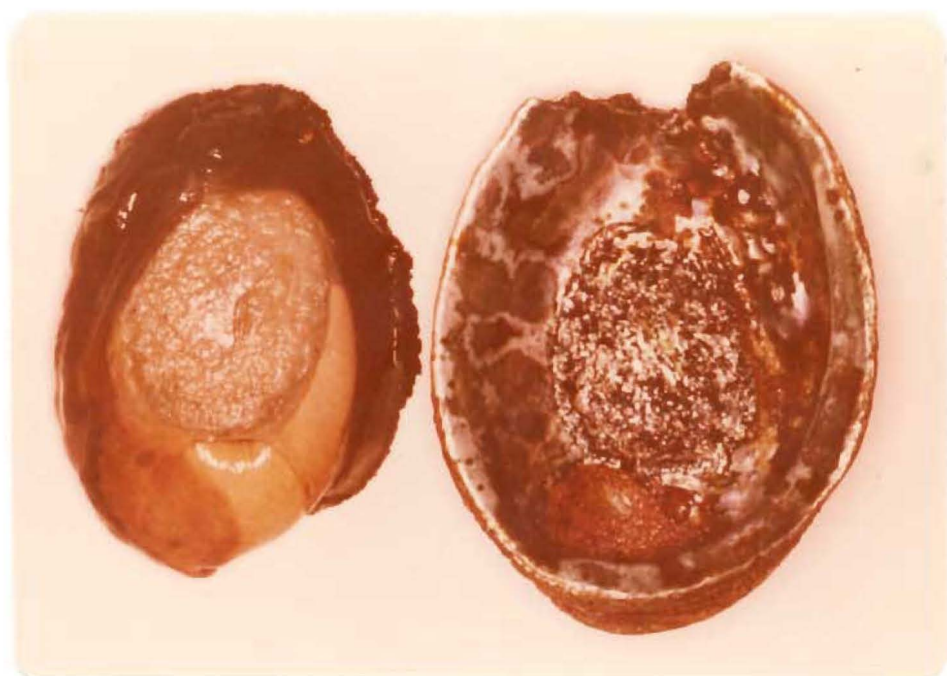
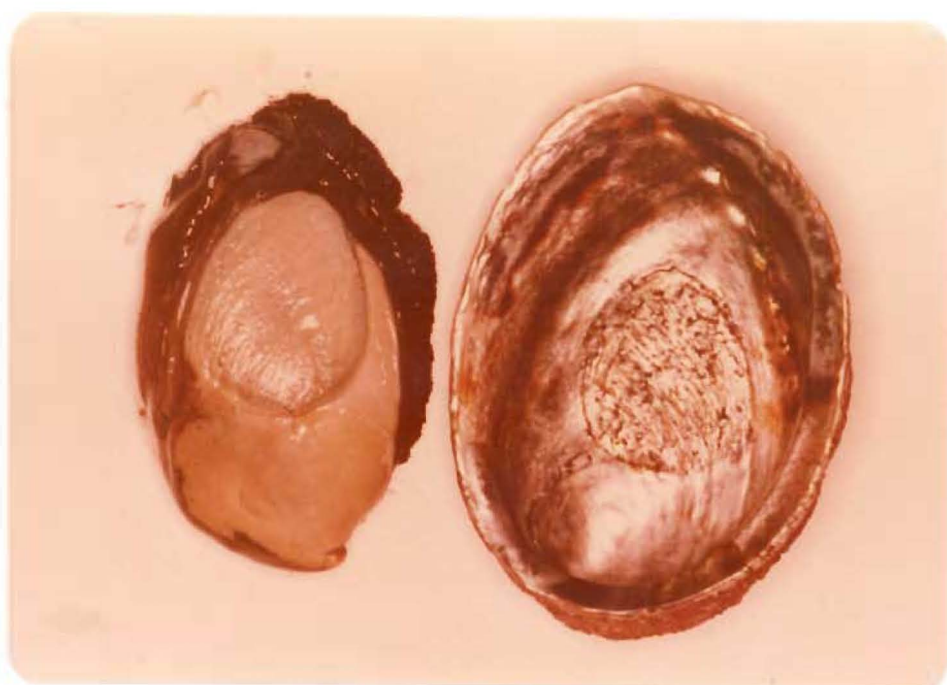
Many of the Banks Peninsula abalones exhibit brown blisters in the nacreous layer of the shell (Fig. 6.1). It was suspected that such animals may have a higher mortality rate than 'normal' abalones since blisters on the muscle attachment surface of the shell (the scar on the inner surface of the shells in Fig. 6.1) greatly reduce the abalone's ability to retain its shell. Even a slight upward pull on some blistered individuals will remove the shell, leaving the naked abalone still attached to the substrate. Often the tissue adjacent to nacre blisters is brown and in some individuals blisters may cover almost all of the inner surface of the shell.



Figure 6.1 Upper: Male *H. iris* from Peraki Bay showing the 'normal' condition of the inner shell surface. Note the muscle attachment scar on the shell surface, and the row of respiratory pores curving from the anterior shell margin to the left of the muscle attachment scar.

Lower: Male *H. iris* from Peraki Bay. Reddish-brown shell blisters have formed in the vicinity of the respiratory pores and shell apex (directly posterior to the muscle scar). The gonad and hepatic gland tissue adjacent to the blisters shows a brown discolouration. The shell of this individual was severely weakened by boring organisms and chipped as the abalone was being removed.

Photo: E. Fordyce



The incidence of nacre blisters in the live population at Peraki Bay was estimated from animals collected for gonad index determination and during the February 1976 transect sampling.

Shells washed up on to the inner beach of Peraki Bay were collected between March 1973 and March 1976 to establish the incidence of blisters among animals which had died. This estimate would be slightly conservative since blistered shells are generally weaker than non-blistered ones, and so are more likely to be destroyed before being washed up on to the beach. If blistered individuals have a greater chance of dying than 'normal' individuals, the incidence of blisters would be higher among those animals which have died than in the live population. The estimates of incidence in live and dead populations were compared to detect any association between the presence of blisters and death.

Eighteen abalone shells were sectioned to establish whether the blisters were associated with penetration of the shell by boring organisms, and several specimens of blistered abalone were sent for examination to Dr B. Jones, an invertebrate parasitologist at Fisheries Research Division of the Ministry of Agriculture and Fisheries.

The shells of two hundred and fifty-eight abalones taken from the Kaikoura region by commercial divers were examined to establish the incidence of shell blisters there.

#### 6.2.3 Results

The results of examination of eighteen sectioned abalone shells were

	hole(s) through shell	no hole(s) through shell
blister present	4	3
blister absent	7	4

While there are too few data to allow statistical analysis, the number of observations in each cell is almost exactly that expected assuming no association between the presence of a shell perforation and the formation of a blister. The presence of observations in all cells suggests that either no simple cause and effect relationship exists between the attributes or that 'instantaneous' observation of the attributes is insufficient to detect it (i.e. those with no hole but showing a blister did have a hole when the blister was formed but it has since been obscured, and those with a hole but no blister will form a blister in time). Dr B. Jones is continuing his examination of the problem, but suggests that blisters may form as a result of irritation by shell boring organisms and/or by sediment trapped between the shell and the mantle.

The numbers of blistered and non-blistered individuals in the samples of live and dead abalones from Peraki Bay were:

	blistered	non-blistered
dead	429	432
live	363	358

There is no significant association between the presence of blisters and death ( $\chi^2 = 0.06$ , d.f. = 1). The same conclusion is reached if the records are separated into three-centimetre size classes.

The incidence of shell blisters in the live population of Peraki Bay was 0.503 ( $N = 721$ ) while at Kaikoura the incidence was only 0.035 ( $N = 258$ ).

The major cause of death of abalones at Peraki Bay appears to be burial by silt when storms cause sudden, localised changes in sediment level. During the summer abalones tend to accumulate near the boulder-silt interface where they feed on drift algae which are common there. If the silt level suddenly rises, these animals are buried, partially buried or forced to move on to the few large boulders which protrude from the silt. Towers of up to five abalones, each clinging to the shell of the animal below it, were sometimes found on these boulders. Such towers are easily toppled, as undoubtedly happens during storms. Abalones were observed moving over short stretches of deep silt, but their adhesion to this substrate was very weak and animals attempting such movement during a storm would probably be washed away, often on to the beach.

In August 1975 observations were made two days after a violent storm during which the sediment level along the boulder beach in the north-eastern corner of Peraki Bay rose vertically by about one metre. Animals in sediment about one centimetre deep seemed healthy, but those surrounded by two centimetres of sediment (still with most of the respiratory pores exposed to sea water) were only weakly attached to the buried boulders. Where the sediment covered the respiratory pores the animals were still alive, but were not attached to the underlying boulders. Even when removed from the sediment and placed on 'clean' rocks they made no

attempt to attach themselves. Ten animals which had been buried in silt were transferred to an aquarium where all died within three days.

Juvenile abalones in the WI and WJ strata were regularly found buried in silt, even in the absence of violent storms. This stretch of coastline is prone to sedimentation since it is sheltered from direct wave action and tidal currents in this area are slow.

Although boulders at Peraki Bay do move during storms, few adult abalones appear to be crushed since empty abalone shells found on the sea-bed were almost invariably whole. Juveniles are probably more liable to be crushed by moving boulders than are adults, but the shells of juveniles are rapidly destroyed after death, making detection difficult.

The only fish observed to eat abalones were banded parrot fish, *Pseudolabrus pittensis*, and then only after human disturbance of the habitat. On six occasions, *P. pittensis* removed young abalones from boulders turned over by divers. The abalones taken were all 30-40 mm long and were eaten whole. Banded parrot fish were never observed to attack the foot or tentacles of adult abalones, even though these are exposed when abalones cling to irregular rock surfaces or catch drifting algae.

On one occasion at Peraki Bay a crab (*Cancer novaezealandiae* carapace width 99 mm) was found eating a 35 mm abalone. The abalone was still alive and attached to the substrate, but the anterior portion of the shell had been chipped away to expose a portion of the foot. At Oteronga

Bay, on the southern coast of Wellington, a 34 mm abalone with a similarly chipped shell was found under the same boulder as a large *Plagusia capense*. Part of the mantle, foot and ctenidia had been eaten. This crab is common at Wellington and Kaikoura but is absent from Peraki Bay.

Large predatory starfish are very rare at Peraki Bay, the only observation being of a single specimen of *Astrostole scabra*. *Astrostole scabra* is known to feed on *H. iris* at Kaikoura (J. Town, University of Canterbury, pers. comm.).

Poore (1969) has suggested that the spiny crayfish, *Jasus edwardsii*, preys upon *H. iris*. Several spiny crayfish were observed during this study, but they showed no evidence of predatory behaviour toward abalones.

#### 6.2.4 Discussion

The causes of death of *H. iris* are similar to those found for other haliotid species. The main predators and their methods of predation are given in Table 6.2.

The main cause of natural mortality among Australian abalones appears to be predation (Shepherd, 1975), while most abalones at Peraki Bay and on the Californian coast (Cox, 1962) are killed by the movement of sediment and boulders during storms. Cox also reported that the attachment of *H. rufescens* to its substrate was weakened by excessive freshwater runoff from the land. This was not observed at Peraki Bay.

Although the observations made at Peraki Bay are probably representative of abalone populations on Banks Peninsula, it is difficult to speculate about the mortality rate of *H. iris*, and its causes, in other parts of New Zealand.

Table 6.2 Predators of haliotids. Authorities: a = Cox (1962);  
b = Poore (1969); c = Shibui (1971); d = Shepherd (1973a);  
e = present study.

<u>PREDATOR</u>	<u>METHOD</u>
Stingrays and eagle rays <i>Myliobatis australis</i> <sup>d</sup> <i>Dasyatis brevicaudata</i> <sup>d</sup>	Crush the shell of adult abalones
Sea otters <sup>a</sup>	Break shell using stones
Fish <i>Pseudolabrus tetricus</i> <sup>d</sup> <i>Pictilabrus lacteolavivus</i> <sup>d</sup> <i>Actinochromis victoriae</i> <sup>d</sup> <i>Scorpaenichthys marmoratus</i> <sup>a</sup> <i>Pseudolabrus pittensis</i> <sup>b,e</sup> <i>Psuedophycis bacchus</i> <sup>b</sup> <i>Ditrema temminckii</i> <sup>c</sup>	Remove small abalones from rocks, some attack exposed portions of the foot of adults
Starfish <i>Coscinasterias calamaria</i> <sup>d</sup> <i>Pisaster</i> spp. <sup>a</sup> <i>Astrostele scabra</i> <sup>b,e</sup>	Attack mainly small abalones
Crabs <i>Plagusia chabrus</i> <sup>d*</sup> <i>Cancer antennarius</i> <sup>a</sup> <i>Plagusia capense</i> <sup>e*</sup> <i>Cancer novaezealandiae</i> <sup>e</sup>	Prise small abalones off rocks; chip shell to expose foot
Crayfish <i>Jasus edwardsii</i> <sup>b</sup>	Chip shell off small abalones; tip moving abalone over.
Octopus <i>Octopus bimaculoides</i> <sup>a</sup> <i>Octopus bimaculatus</i> <sup>a</sup> <i>Octopus flindersi</i> <sup>d</sup> <i>Hapalochlaena maculosa</i> <sup>d</sup>	Drill small holes through abalone shell
Whelks <i>Thais baileyana</i> <sup>d</sup> <i>Thais orbita</i> <sup>d</sup>	Drill small holes through shell

\* *Plagusia chabrus* may be a synonym of *Plagusia capense* (Bennett, 1964)



The major causes of mortality undoubtedly vary with locality. Populations on rocky coasts, such as in the Wellington and Kaikoura regions, are probably not subject to the effects of moving sediment to the extent of the Peraki Bay population, but they are generally exposed to stronger wave action and to larger populations of predator species (notably of *Plagusia capense* and *Astrostele scabra*). Increased predation is probably only relevant to the survival of small *H. iris*, and in the absence of moving sediment, abalones larger than about 70 mm may have a higher survival rate at Wellington and Kaikoura than they do on Banks Peninsula.

It may be that rays (e.g. *Zearaja nasuta*) in New Zealand, like those in Australia, prey upon abalones although no observations of this have been recorded.

## 7. POPULATION DYNAMICS AND EXPLOITATION OF *H. IRIS*

### 7.1 RECRUITMENT PATTERN AND SIMULATION OF THE PERAKI BAY POPULATION

#### 7.1.1 Introduction

The size structure of the Peraki Bay abalone population in February 1976 was strongly skewed to the left (see Chapter 2, Fig. 2.5), indicating that many old animals and very few young were present. To maintain the 1976 population at the observed level of about 179 000 individuals with an annual instantaneous mortality rate of 0.1, an annual recruitment of about 17 000 two year olds would be necessary. The estimated annual recruitment during the time encompassed by the present study was only 2000 - 5000, and because it is unlikely that sampling bias could have resulted in a three - eight fold underestimate recruitment, it must be concluded that recruitment to Peraki Bay between February 1974 and February 1976 was well below the level responsible for establishment of the 1976 *H. iris* population. Thus it is instructive to examine the effects of various patterns of recruitment on the population size structure; the object being to determine the type of pattern likely to have resulted in the size structure observed at Peraki Bay in 1976. The effects of recruitment patterns on the size structure were examined by population simulation using the size class population model presented in Chapter 1.

### 7.1.2 Methods

An annual size class projection matrix was constructed using the growth parameters given in Chapter 3 and an annual instantaneous mortality of 0.1. The equations given in Chapter 1 were used iteratively to obtain the population size structure at yearly intervals, beginning with 179 000 animals uniformly distributed among 150 one millimetre size classes. (The results presented could be obtained from any starting population structure.) The calculations were performed by a computer programme similar to that given in Appendix 7.1, except that recruits were added to the population at the end of each time period (year) and there was no fishing mortality. Recruitment was treated as being independent of the adult stock, and recruits were considered to be two years old when they entered the population, i.e. the length frequency distribution of recruits was normal with mean 42 mm and standard deviation 6.5 mm (see Chapter 3).

Simulations using five patterns of recruitment are presented here, and in each case the long-term mean recruitment was fixed at 17 000 two year olds per year so that the number of animals in the starting population is ultimately maintained. This measure was introduced so that interpretation of the simulations could be made without regard to long-term growth of the simulated population. The mean level of recruitment chosen for the simulation would affect the absolute number of animals in each size class and in the total population at any time, but not the proportionate abundance of each size class or the overall

pattern of change. The recruitment patterns used were:

- i) Uniform random (pseudo-random variable taking values between 0 and 34 000).
- ii) Sine wave with 10 year period (range of recruitment 0 to 34 000).
- iii) Pulse of strong recruitment with a 10 year period (recruitment increased rapidly during a pulse, and then it rapidly decreases and remains at a low level until the next pulse; range of recruitment 2000 to 60 000).
- iv) Sine wave (as in ii) with 20 year period.
- v) Pulse (as in iii) with 20 year period.

The effects of possible random variation superimposed upon patterns ii through iv were examined by separate simulations in which recruitment at any time varied uniformly randomly between  $\pm 50\%$  of the level given by each pure pattern.

The size structure resulting from constant recruitment is examined in connection with the yield per recruit analysis in section 7.3 (Fig. 7.11) and so is not repeated here. The main criterion for comparison of the simulated and actual population structures is the degree of skew to the left, and so  $g_1$ , the coefficient of skewness (Snedecor and Cochran, 1967), was calculated for all population structures. The coefficient of skewness is the third moment of the distribution divided by the  $3/2$  power of the second moment, and is positive for a skew to the right and negative for a skew to the left. The value of  $g_1$  for the Peraki Bay abalone population in February 1976 was  $-1.486$ .

Another subjective criterion is the degree to which the simulated structures exhibit the strong numerical dominance of 100-120 mm animals evident at Peraki Bay in 1976.

### 7.1.3 Results

Typical results of the simulations are given in Figs 7.1 to 7.6. In all cases at least 70 years have elapsed between the initial population and the beginning of the sequence presented, so that few individuals ( $< 0.1\%$ ) from the initial population contribute to the size structures given.

Uniform random recruitment (Fig. 7.1) is unlikely to result in a population size structure similar to that observed at Peraki Bay in February 1976. At times the size structure may be skewed to the left as a result of years of poor recruitment (e.g. at  $t = 94$  in Fig. 7.1), but none of the simulations examined (representing 280 years) resulted in a size structure as strongly skewed to the left as that observed in the field. A series of years of very good recruitment followed by many years of very poor recruitment are necessary to produce such a size structure, and these combinations are highly unlikely if recruitment is uniform random.

There was also poor agreement between the actual and predicted population structures when recruitment followed a sine wave with a period of 10 years (Fig. 7.2). Random variability of the type examined did not appreciably improve the agreement, although again, rare sequences of events could conceivably result in size structures similar to those observed at Peraki Bay.

Figure 7.1    Simulation of the Peraki Bay abalone population when recruitment varies uniform randomly. The  $g_1$  statistic is the coefficient of skewness, and decreases with increased skew to the left.

$g_1 = -1.48$  for the Peraki Bay population in February 1976.

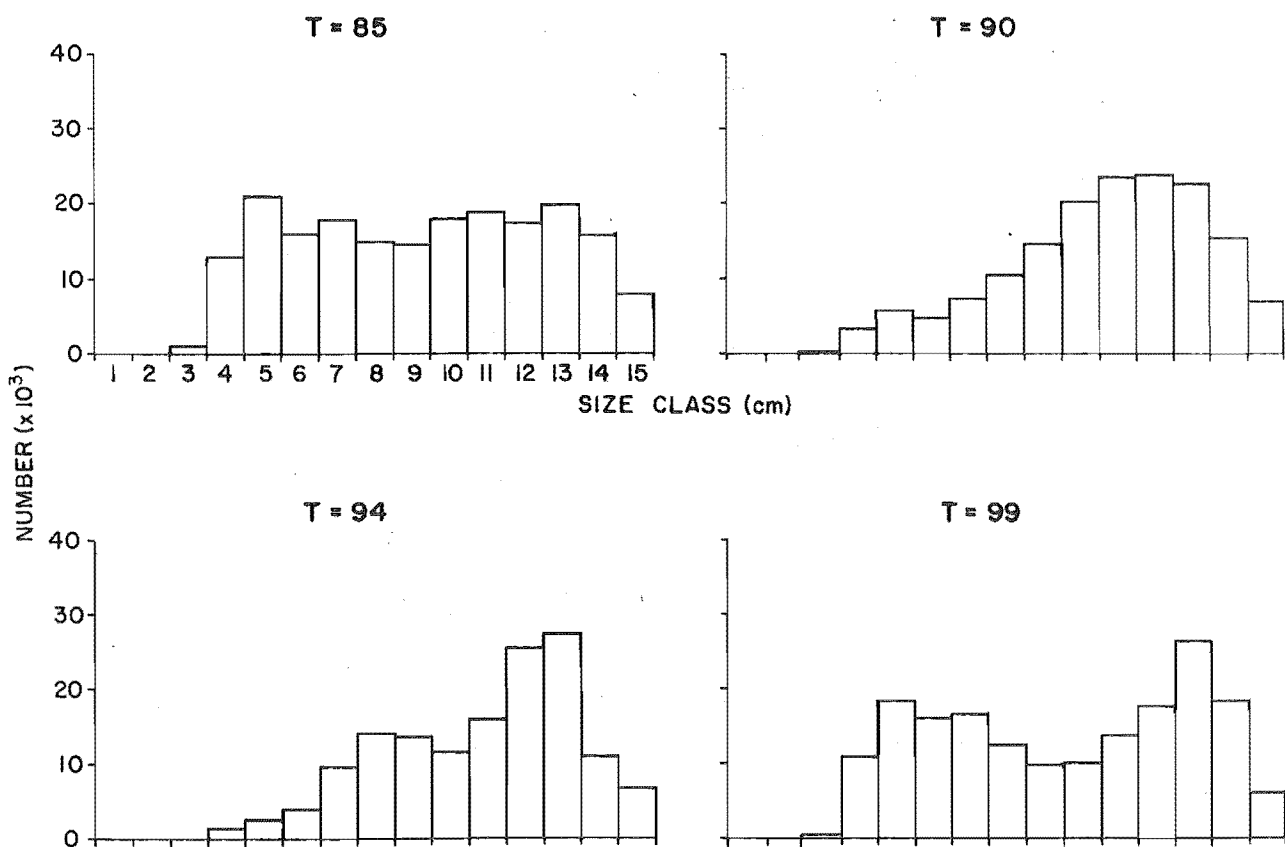
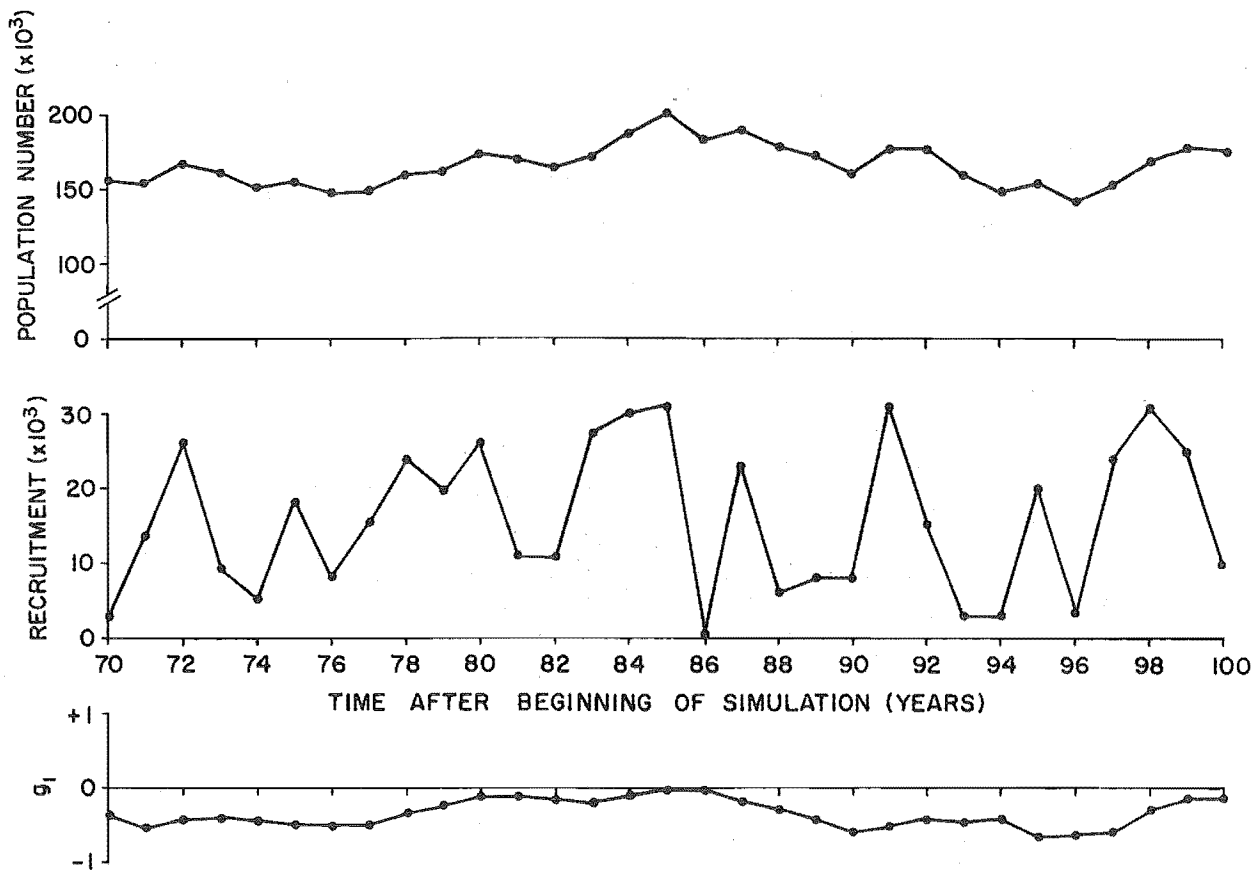


Figure 7.2    Simulation of the Peraki Bay abalone population when recruitment follows a sine wave with a period of 10 years.  $g_1$  is the coefficient of skewness and equals  $-1.48$  for the Peraki Bay population in February 1976.



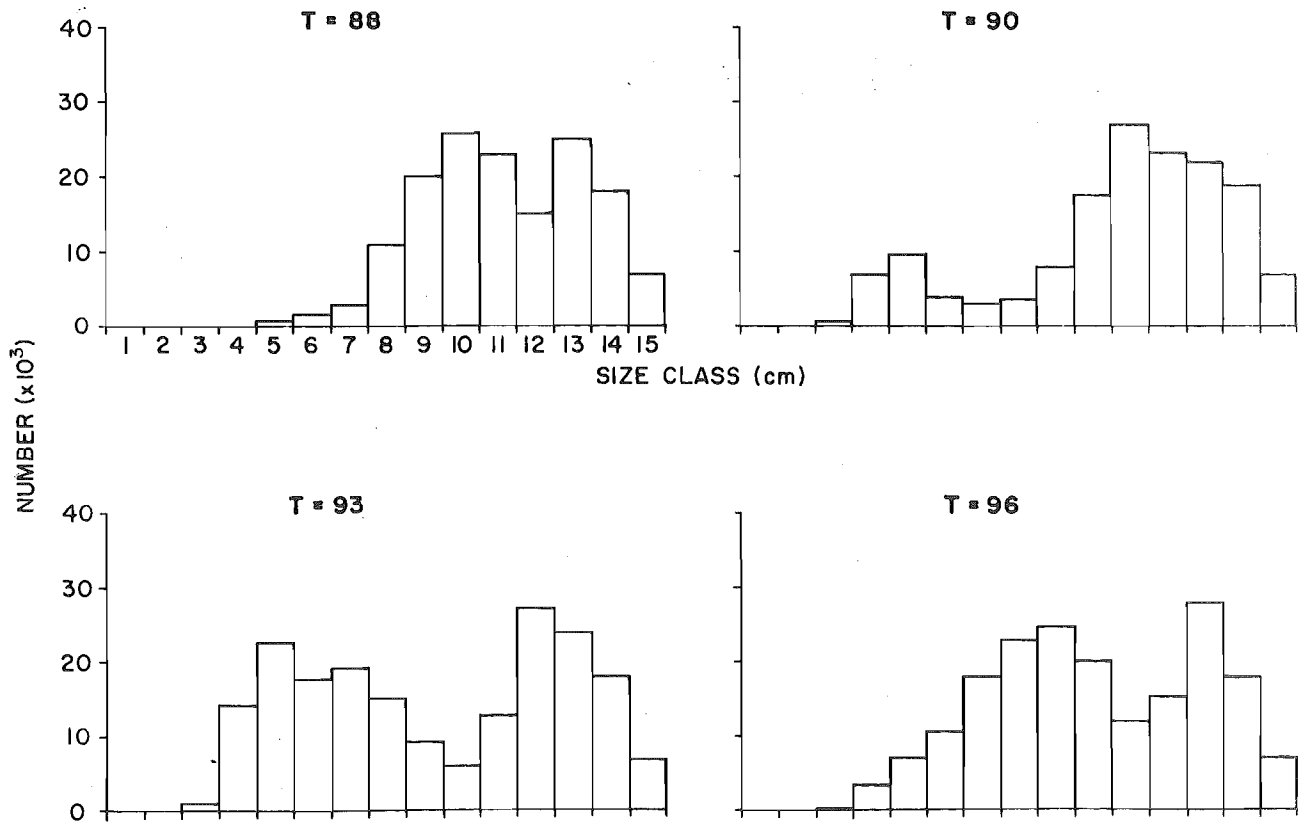
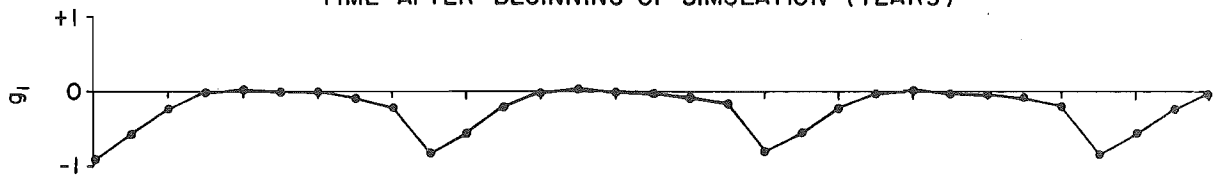
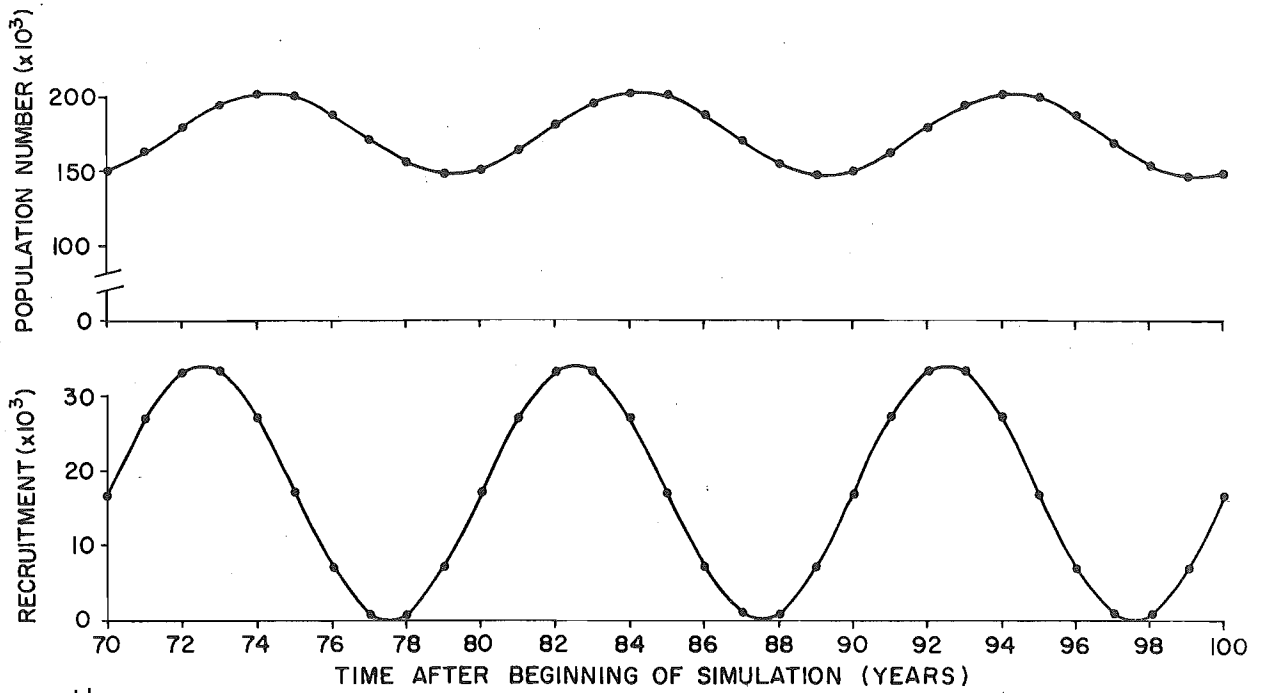


Figure 7.3    Simulation of the Peraki Bay abalone population when a pulse of good recruitment occurs every 10 years.  $g_1$  is the coefficient of skewness and equals  $-1.48$  for the Peraki Bay population in February 1976.

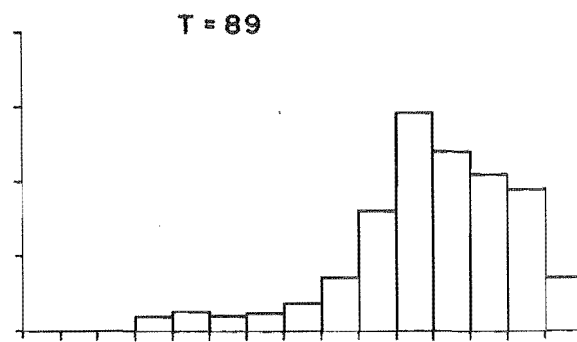
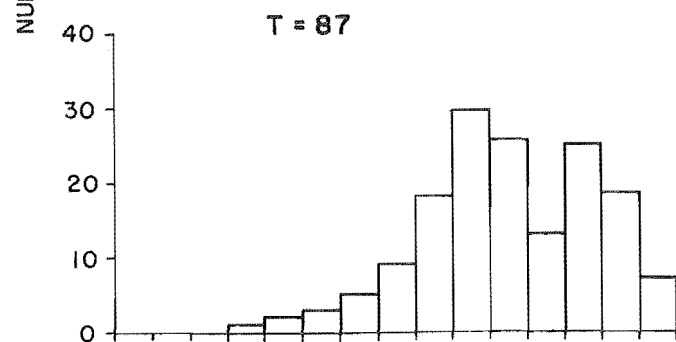
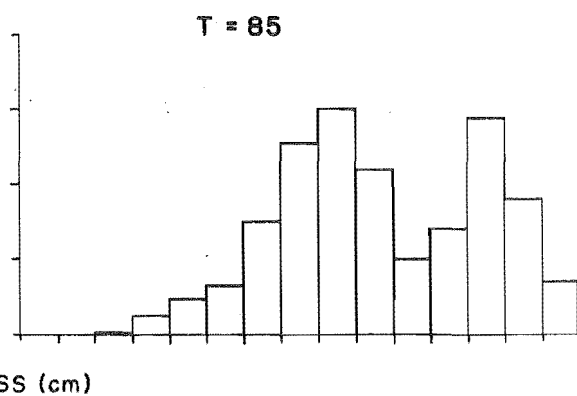
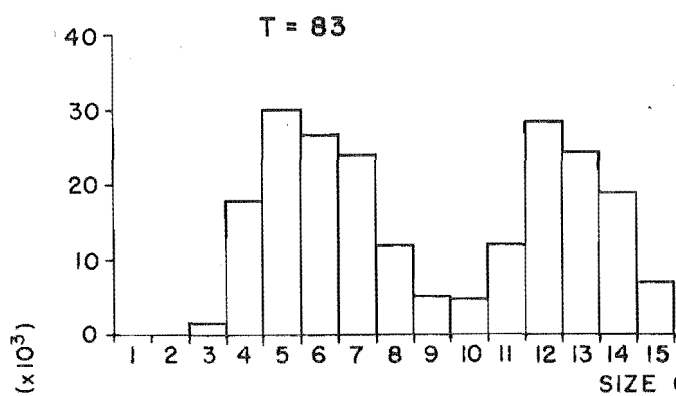
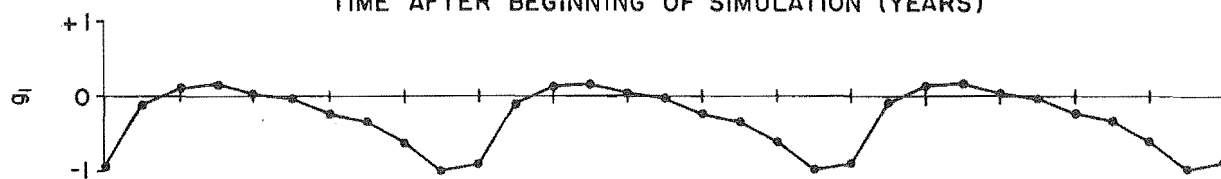
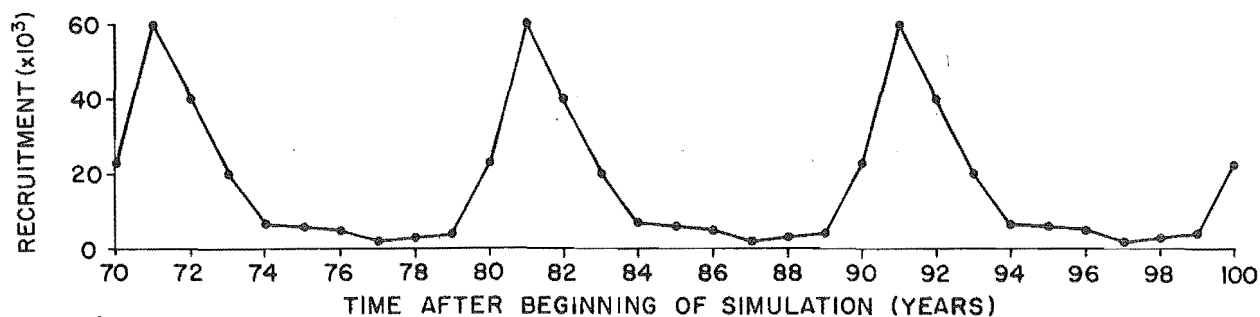
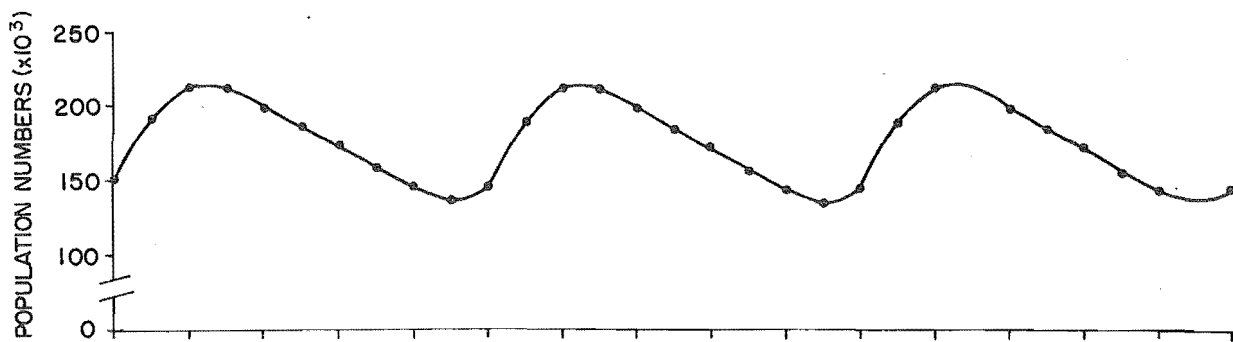


Figure 7.4    Simulation of the Peraki Bay abalone population when recruitment follows a sine wave with a period of 20 years.  $g_1$  is the coefficient of skewness and equals  $-1.48$  for the Peraki Bay population in February 1976.

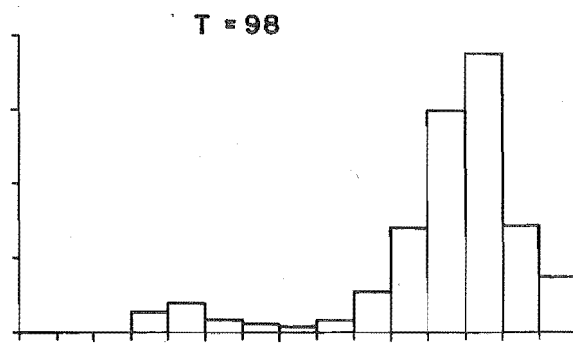
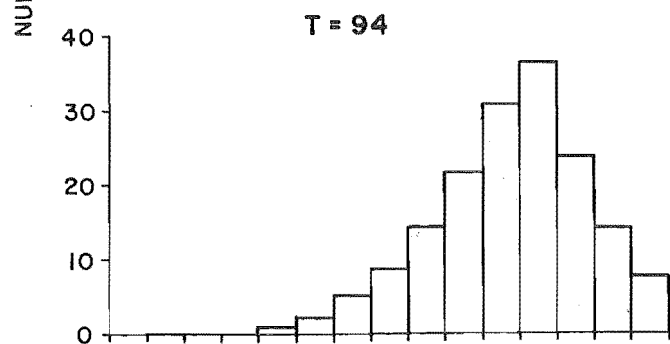
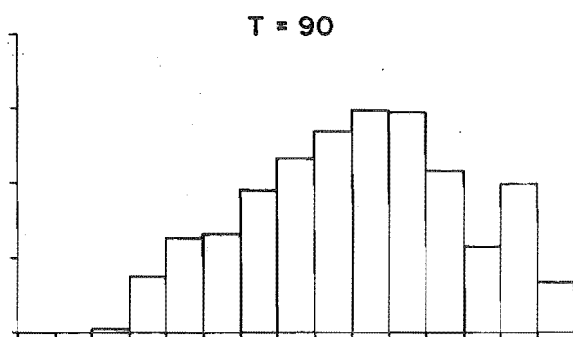
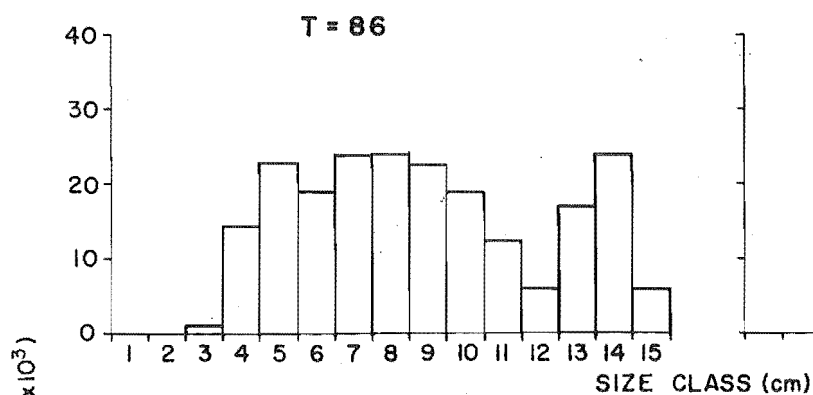
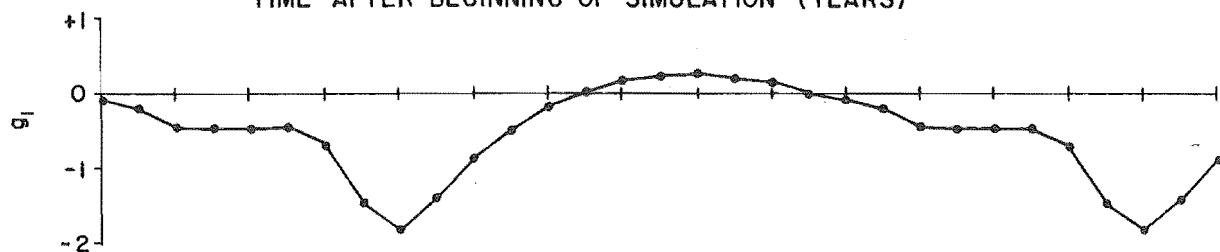
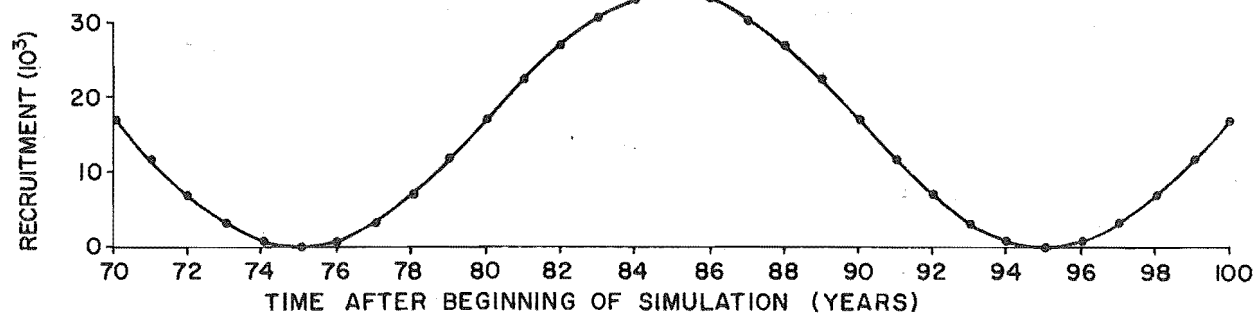
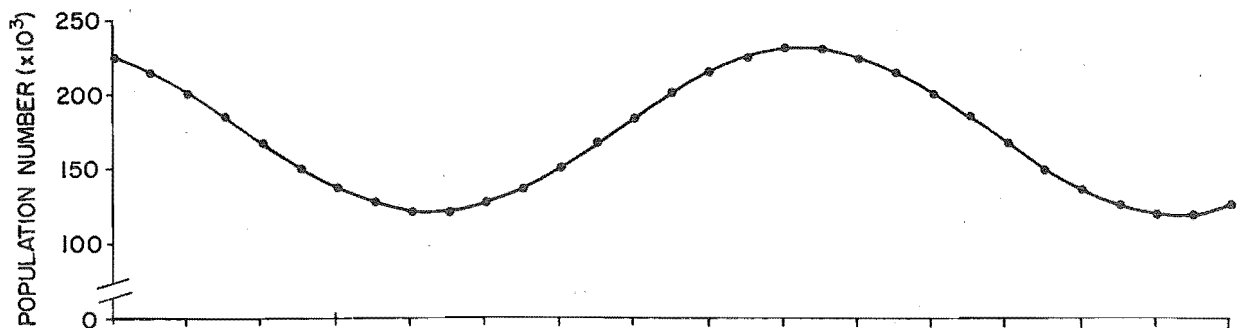


Figure 7.5    Simulation of the Peraki Bay abalone population when a pulse of good recruitment occurs every 20 years.  $g_1$  is the coefficient of skewness and equals  $-1.48$  for the Peraki Bay population in February 1976.

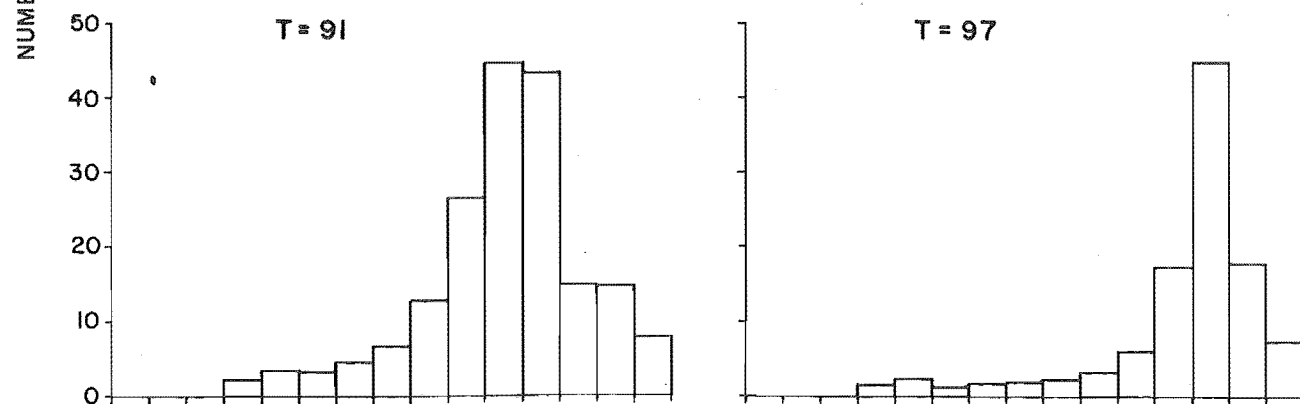
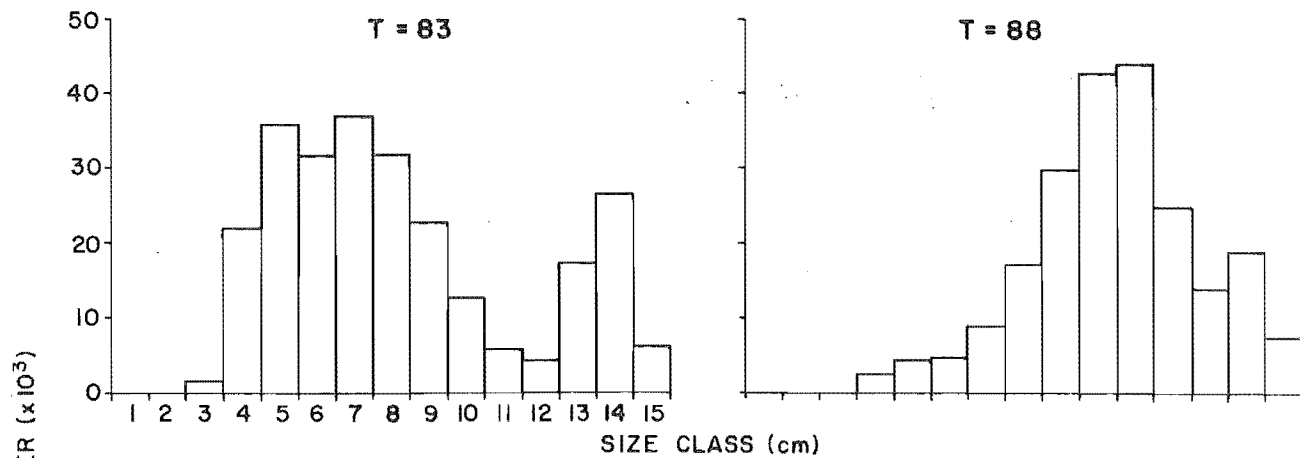
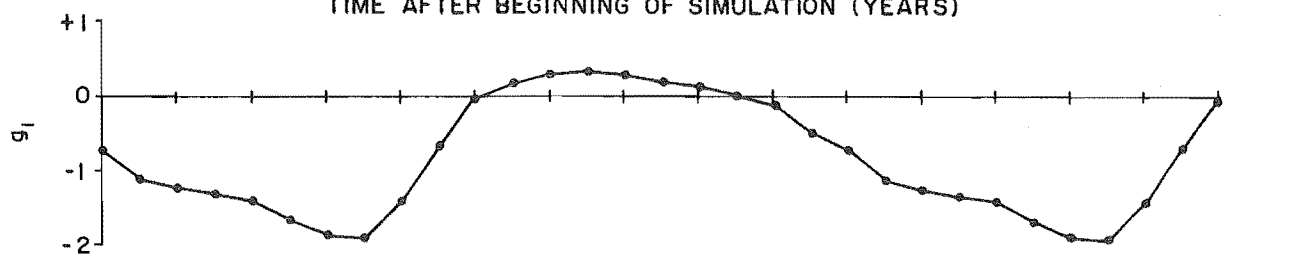
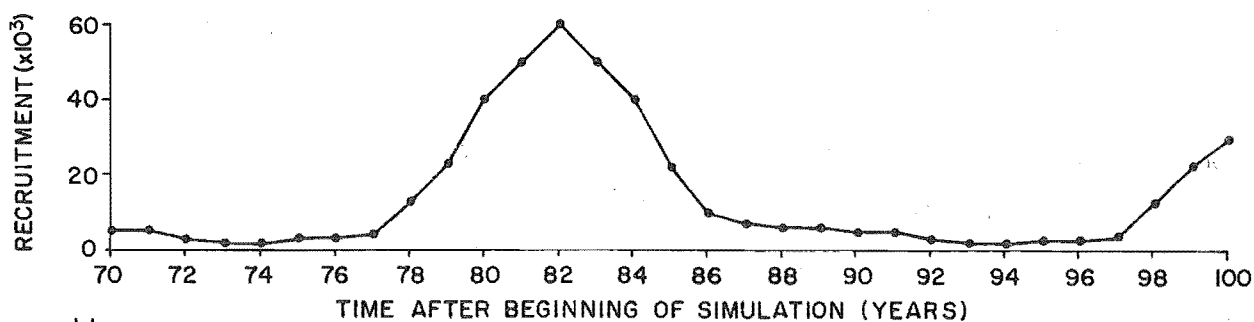
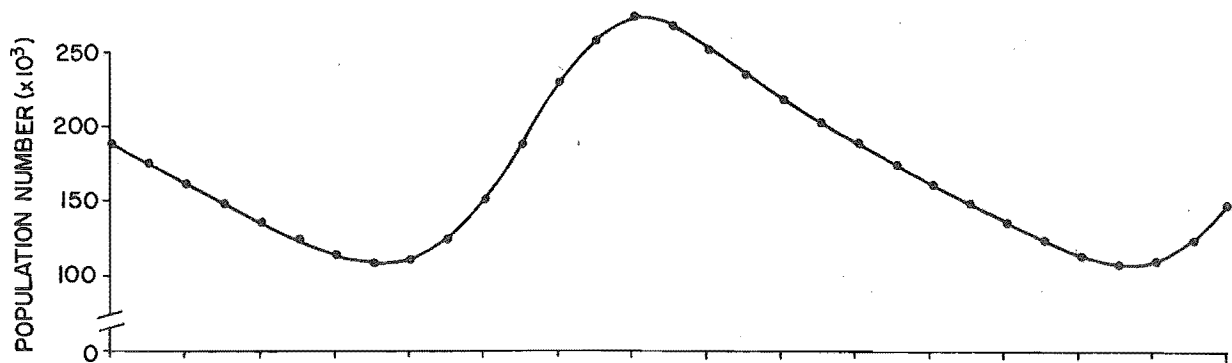
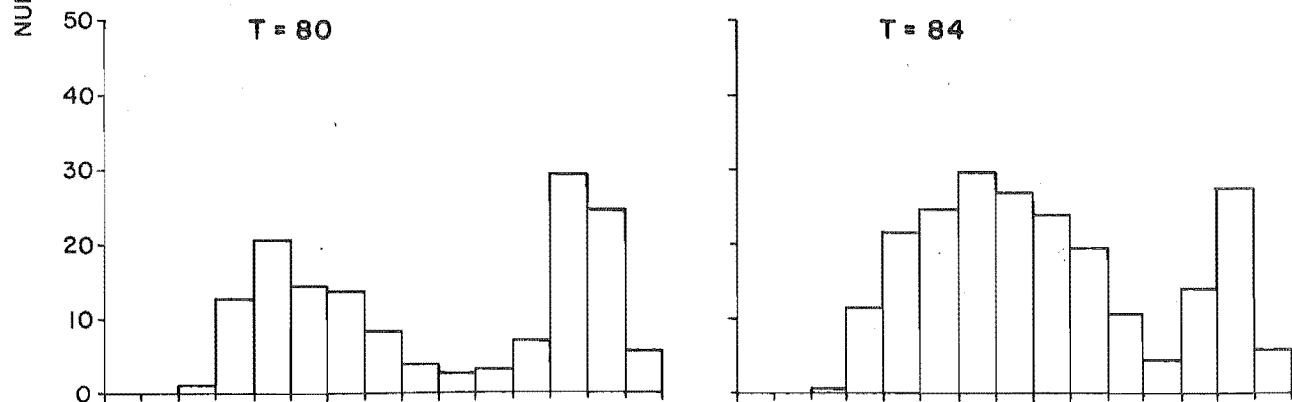
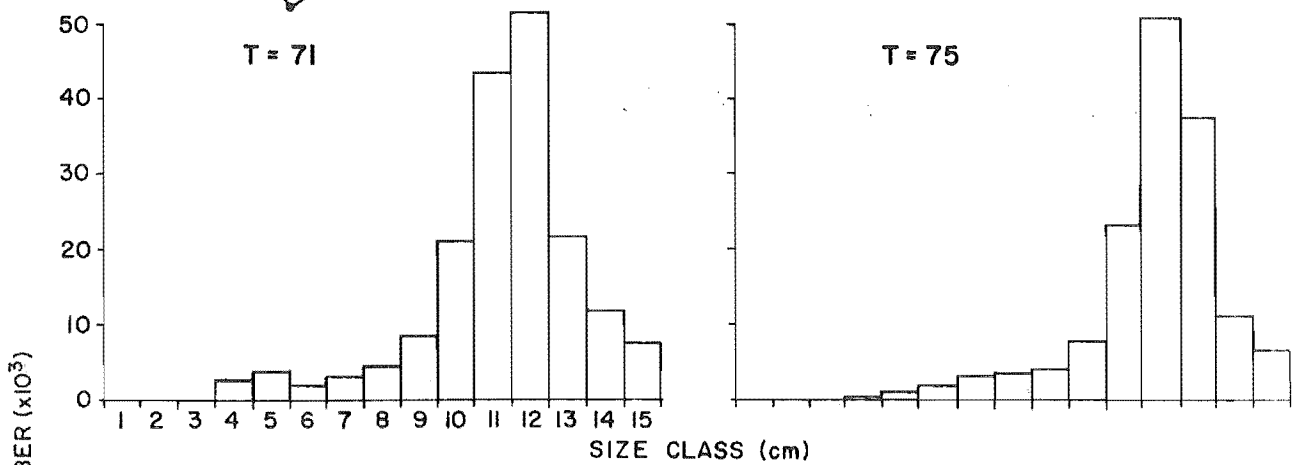
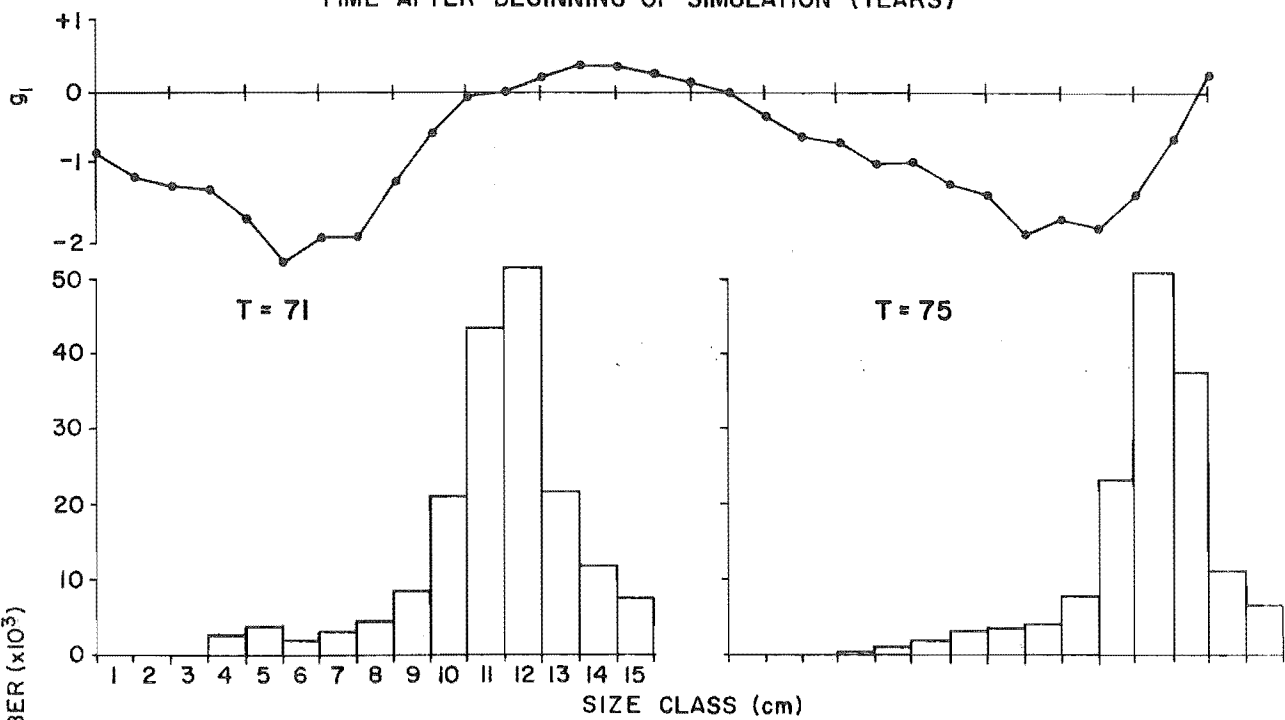
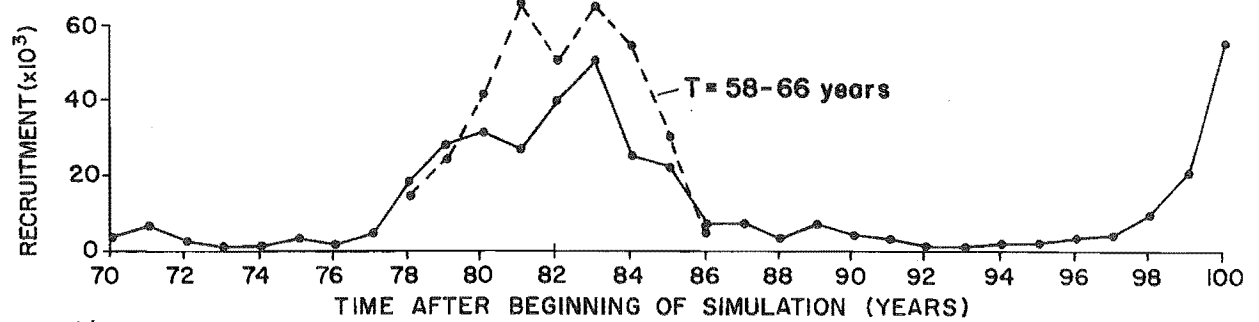
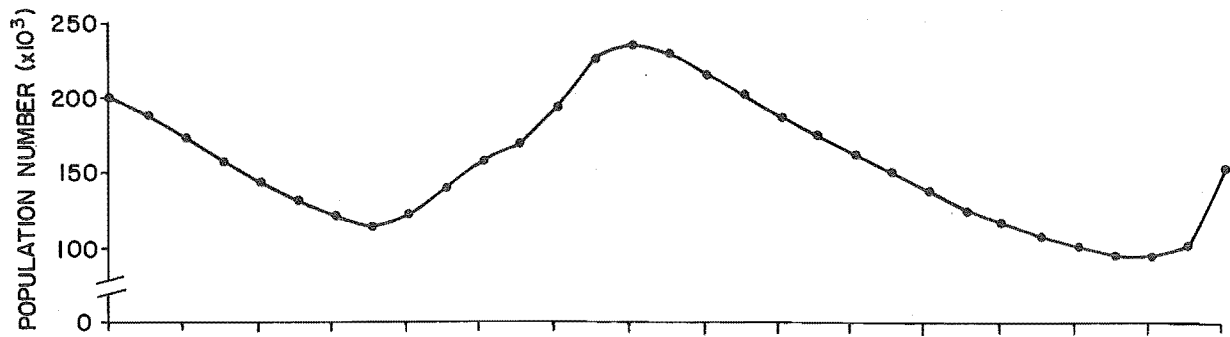


Figure 7.6 As for Figure 7.5 with a random element  
superimposed upon the pure pattern of recruitment.





A pulse of good recruitment with a period of 10 years (Fig. 7.3) seems slightly more likely to result in the observed structure than a pure sine wave but it still does not result in the strong numerical dominance of 100-120 mm animals observed to be the case at Peraki Bay.

Changes in recruitment with a period of 20 years result in generally better agreement between the observed and predicted size structures than do the same changes with a period of 10 years. The population size structure was, at times, strongly skewed to the left when recruitment followed a sine wave with a period of 20 years (Fig. 7.4), but even with the introduction of random variability the numerical dominance of 100-120 mm animals was not as marked as it was in the actual population. A pulse of strong recruitment with a period of 20 years resulted in the best agreement between the simulated and actual population size structure of any of the patterns examined. Even without superimposed random variability the simulated size structure remained similar to that observed at Peraki Bay for several years of each cycle (Fig. 7.5). The introduction of a random element frequently resulted in population size structures extremely close to that observed in the field (Fig. 7.6).

#### 7.1.4 Discussion

The results of the simulations must be interpreted with caution. Patterns of recruitment other than those examined, as well as random variation (other than the type used) superimposed upon any of the patterns examined, could result in size structures similar to those observed at

Peraki Bay; particularly in view of the large sampling variability associated with field estimates of the size structure. However, it is reasonably certain that the observed size structure of abalones at Peraki Bay in 1974 resulted from a period of very high recruitment, which was both preceded and followed by periods of low recruitment, and that this fluctuation took place over a time period of about 20 years, with the peak of high recruitment occurring some 10-15 years before 1976. This suggested history of recruitment applies only to Peraki Bay (although it could apply to neighbouring bays), which is in a poor geographical position to receive recruitment via the dominant current system in the area (see Chapter 5). Good recruitment to Peraki Bay may be more dependent on rare combinations of wind and current conditions than is the case in areas such as Kaikoura. Future trends in recruitment to Peraki Bay cannot be deduced from the simulations because it is unknown whether the suggested historical trend is cyclic, random about some mean value (with a non-uniform distribution) or follows some other pattern. However, the suggested recruitment pattern (short periods of very high recruitment occurring between long periods of low recruitment) carries with it certain implications concerning the population structure and these may be examined by further sampling of the Peraki Bay population after a reasonable length of time has elapsed (say about 10 years). A peak of strong recruitment should be present by such time and the population should be similar to that shown on the upper left histograms of Figs 7.4 and 7.5.

If the present period of low recruitment continues for a further 10 years, the population structure should be severely skewed to the left, with a strong numerical dominance of 120 mm - 140 mm individuals. The total population should have declined to about 90 000 individuals.

It is interesting to note that the population model consistently predicts more animals in the 130-150 mm size range to be present than were apparent in the actual population. This could be due to the way in which the study population was defined, i.e. to include abalones only within Peraki Bay. Many large abalones occur on the exposed headlands between bays on Banks Peninsula, and because the habitat there is unsuitable for juveniles these large animals are probably migrants from the 'within bays' populations. Length frequency structures, based on samples from both headlands and within bays, would probably contain more animals in the 130-150 mm size range (i.e. would look more like the simulated population structures) than is the case when samples are taken only from within a bay. Other possible explanations of this discrepancy between the simulated and actual population structure are:

- a) Some inappropriate assumptions made during construction of the model (e.g. the treatment of growth)
- b) The use of incorrect parameters in the growth function (e.g. the estimates of  $L_{\infty}$  and/or  $K$  are too large)
- c) Mortality among large animals being higher than 0.1

- d) The existence of temporal fluctuations in the growth and/or mortality rates.

## 7.2 SUMMARY OF THE POPULATION DYNAMICS OF *H. IRIS*

The population parameters of *H. iris* vary both in time and space. Abalones at Kaikoura reach a greater maximum size and show a faster growth rate than those on Banks Peninsula. The parameters of the Von Bertalanffy growth equation are  $K = 0.310$ ,  $L_{\infty} = 146$  mm for *H. iris* at Kaikoura (Poore, 1972c) and  $K = 0.164$ ,  $L_{\infty} = 131$  mm for those at Peraki Bay. Growth at both Kaikoura and Peraki Bay is most rapid during summer-autumn, although seasonality of growth rate is more pronounced at Peraki Bay where, during some years at least, most of the annual growth increment may be produced during the autumn. The differences in growth between localities may be due to differences in the availability and quality of algal food species.

The annual survival of *H. iris* at Peraki Bay is high; about 80-95% of the animals older than 2 years of age survive each year. An annual survival of about 90% implies that maximum longevity under field conditions is in excess of 30 years and that the recruits in any year will live to an average age of 11.5 years. Aspects of the physical environment (notably changes in sand level associated with storms) are the chief causes of death at Peraki Bay, whereas death through predation (by crabs, fish and starfish) seems relatively rare. The abalones at Kaikoura are probably less liable to burial by sand, and so the

survival rate of adults there may be greater than for those at Peraki Bay. However, juvenile survival rates may be lower at Kaikoura than at Peraki Bay since predatory species of crabs and starfish are more abundant at Kaikoura.

Fecundities of *H. iris* from Kaikoura are considerably higher than those from Peraki Bay. Female abalones at Kaikoura first produce significant numbers of eggs when 90-100 mm in length (4-5 years old), whereafter fecundity rapidly increases with increasing size, reaching about 11 million eggs per 150 mm female (Poore, 1972d). Females at Peraki Bay also first produce significant numbers of eggs when about 90 mm in length, but this corresponds to an age of about 7 years. Fecundity of females at Peraki Bay rapidly increases with length for individuals between 90 and 110 mm, but levels off over the size range 110-130 mm to a fecundity of about 1 million eggs per female. Animals over 130 mm in length exhibit slight reproductive senescence. Spawning takes place in late summer-early autumn, and abalone at both Kaikoura and Banks Peninsula fail to spawn in some years. No reason for this failure can be offered. Larval *H. iris* are planktonic for 5-10 days and during this time may be transported far from the parent stock. The speeds and directions of currents in the sea are therefore very important and their highly variable nature, combined with the vagaries of larval behaviour (i.e. orientation, depth preference, vertical migration), make only broad statements on larval dispersal possible. Generally, however, the Peraki Bay population probably receives most of its recruitment from abalones living on the coast of

Oamaru, while larvae produced on Banks Peninsula most likely settle between the Waipara River and Kaikoura. The bulk of recruitment to Kaikoura probably comes from adults living between the Waipara River and Hamuri Bluff (about 30 km south of Kaikoura). Some larvae undoubtedly travel in directions opposite to these general trends and some may remain very close to the parent stock. It is likely that the speed and direction of transport varies greatly between years.

The size structure of the Peraki Bay abalone population in 1976 probably resulted from a short (about 5 year) period of high recruitment about 10-15 years before 1976, preceded and followed by periods of low recruitment. It is not known whether this is part of some long-term cycle, 'random' variation or part of some other trend. In any case the size structure of the Peraki Bay population would be expected to alter considerably with time. The distribution of abalone stocks and the current system along the east coast of the South Island of New Zealand suggest that recruitment to the Kaikoura population is likely to be less variable than recruitment to the Peraki Bay population. Thus the size structure of the Kaikoura population may be less variable than that of the Peraki Bay population.

### 7.3 YIELD PER RECRUIT ANALYSIS AND EXPLOITATION

#### 7.3.1 Introduction

The population model described in Chapter 1 cannot be fully employed to analyse the abalone fishery because

the effects of population density on the various parameters of the model are not known. The fishery can, however, be examined in terms of the yield per unit recruitment. This is the total yield which will eventually be obtained from some arbitrary number of recruits entering the population and being subjected to a particular fishing regime throughout their lives. It may be obtained by summing the annual yield taken from the recruits in successive years from the time of recruitment until the number remaining is zero or negligible (see Beverton and Holt, 1957; Ricker, 1958). The yield per recruitment calculated in this way is not affected by variability in recruitment since it simply provides the ultimate yield obtained from whatever number of units of recruitment enter the population. This yield equals the total annual yield per unit recruitment from the whole population under equilibrium conditions [i.e. conditions which have been constant 'long enough to affect all ages for the whole of their exploited life' (Ricker, 1958); this equals the 'steady state' of Beverton and Holt, 1957)].

The yield per recruit may be calculated for a range of fishing policies (usually combinations of fishing mortality and minimum legal size) to determine which policy or policies result in the maximum yield per recruit.

Since the nature of the fishing policy ultimately affects the population density, which may in turn cause a change in the growth or mortality rate, it must be assumed that growth and mortality do not alter over the range of population densities associated with the fishing regimes



examined. Probably the most crucial weakness of yield per recruit analysis is that it provides no indication as to how sustainable a given level of exploitation might be, i.e. it provides the ultimate yield from a given number of recruits but not the ultimate number of progeny produced by them. This 'sustainability' is extremely important, particularly since the most common cause of the collapse of a fishery is failure of recruitment (Gulland, 1973).

The Kaikoura and Banks Peninsula abalone fisheries are examined in terms of their yield per recruitment, and the equilibrium size structure under various fishing regimes is given. The expected reproductive life of a recruit entering the population is also estimated for various fishing regimes.

#### 7.3.2 Methods

A computer programme was written (Appendix 7.1) which calculates the yield per unit recruitment from the equations given in Chapter 1, and utilising estimated parameters of growth and mortality. The programme constructs the size class projection matrix (without recruitment terms) and iteratively follows the fate of a given number of recruits (in this case 1000) by calculating, at yearly intervals, the number of animals remaining of the original recruitment, their size frequency and the yield taken from them during the preceding year. This process was repeated until less than 1% of the initial recruitment remained. The yield per initial number of recruits was calculated as the sum of the annual yields. The equilibrium age and size structure of the post recruit population was obtained by

combining the relevant annual structures, i.e. the equilibrium age structure was given directly from the number of animals surviving from recruitment to each age and the size structure was obtained from

$$N_j = \sum_{t=0}^{t=\lambda} N_{j,t}$$

where  $N_j$  is the equilibrium number of animals in size class  $j$  (per unit recruitment),  $N_{j,t}$  is the number of original recruits in the  $j$ th size class  $t$  years after recruitment and  $\lambda$  is the number of years a significant proportion (0.01) of the recruitment remains in the population. The expected number of spawnings that a 2 year old recruit will ultimately have the opportunity to participate in (ES) was calculated from the survivorship ( $S_x$ ).  $S_x$  is the number of animals surviving from the age of recruitment (2) to age  $x$ .

If breeding first occurs at age  $b$  (7 years at Peraki Bay, 4 years at Kaikoura) and there are no post-reproductives,

$$ES = \frac{\sum_{x=b}^{x=\lambda} S_x}{S_2}$$

where  $S_2$  is the initial number of recruits. ES simply gives the expected number of spawning seasons to be experienced per recruit. It does not take in account the possibility of years in which the population does not spawn, nor does it include the changes in fecundity with size. ES is similar to a net reproductive rate (see, for example, Mertz, 1970) except that reproduction is measured by the number of spawnings rather than by the resulting number of

progeny (i.e.  $M_x$  in the life table is unity for all animals of breeding age and zero otherwise).

Yield per recruitment isopleth diagrams were constructed for both the Kaikoura and Banks Peninsula fisheries. During initial testing one millimetre size classes were used, but it was found that the size class width could be increased to ten millimetres without seriously affecting the resulting estimates. Since this increase in size class width resulted in a considerable saving of computation time, all estimates provided here were calculated using ten millimetre size classes.

The Banks Peninsula fishery was examined using the growth and mortality parameters estimated for the Peraki Bay population. The mean annual growth increment of animals less than 60 mm was obtained from the results of the juvenile length frequency analysis (Fig. 3.4), while for larger animals it was calculated using the modified Von Bertalanffy growth equation (Appendix 3.2) with  $L_\infty = 131.9$  mm,  $\sigma_{L_\infty}^2 = 138.7$  mm,  $K = 0.1636$  and  $\sigma_K^2 = 0.0118$ .

For all size classes the growth increment was assumed to be normally distributed about the mean, and the variance was calculated from the modified Von Bertalanffy equation. Yield per recruitment isopleth diagrams were constructed for each of four levels of annual instantaneous natural mortality; 0.05, 0.1, 0.15 and 0.2. Yields in numbers were converted to yields in foot weight (g) using the polynomial length-weight equation given in Chapter 3. Analysis of the Kaikoura fishery utilised data

provided by Poore (1969, 1972c), i.e.  $L_{\infty} = 146.2$  mm,  $K = 0.3104$  and the length-body weight (including viscera) relationship  $W = 0.000145 L^3$  (applied only to animals larger than 110 mm). The values of  $\sigma_{L_{\infty}}^2$  and  $\sigma_K^2$  for abalone at Kaikoura were assumed to be the same as for the Peraki Bay population. Separate analyses were made using annual instantaneous natural mortality rates of 0.1 and 0.2. Because the values of the growth parameters assumed for the Kaikoura population are unlikely to be exact, the Kaikoura yield per recruitment isopleth diagrams must be regarded as approximate.

Recruitment to both the Kaikoura and Banks Peninsula populations was taken to occur at two years of age, i.e. the length-frequency distribution of recruits when they entered the population had mean 42 mm and standard deviation 6.5 mm. The Banks Peninsula fishery was examined for minimum legal sizes of 80 mm to 130 mm in steps of 10 mm, and the Kaikoura fishery was examined over the range 100-140 mm in steps of 10 mm. Yield per recruitment for both fisheries was calculated using annual instantaneous fishing mortalities of from 0.1 to 1.0 in steps of 0.1. The upper limit examined corresponds to the estimated fishing mortality among abalones on a heavily exploited Australian reef (Beinnsen, 1976) and is probably attainable under New Zealand conditions. Fishing mortality was assumed to be 'knife-edge' with respect to size, i.e. animals below the minimum legal size experienced no fishing mortality and the full fishing mortality is applied to all individuals above the minimum legal size. This assumption

is probably reasonable, particularly in areas where fishing is intense (see Witherspoon, 1975).

### 7.3.3 Results

Yield per recruitment isopleth diagrams for the Banks Peninsula fishery and the effects of exploitation on the expected number of breeding opportunities per recruit are given in Figs 7.7 to 7.10. Each yield per recruitment isopleth diagram is a 'contour map' of yield per recruitment for pairs of fishing mortality ( $F$ ) and minimum legal size values. The minimum legal size which results in the highest yield per recruit for any given fishing mortality (i.e. eumetric fishing, see Beverton and Holt, 1957) is readily obtained from each diagram. Inspection of Figs 7.7 to 7.10 reveals that for any given fishing mortality the optimal minimum legal size and the maximum yield per recruitment attainable decreases with decreasing natural mortality ( $M$ ). This is to be expected because the yield per recruitment is a balance of growth and death. Under low natural mortalities few animals are lost to natural causes and so it is advantageous to wait until the animals reach a large maximum size before they are taken by the fishery. However, considerable biomass will be lost during such a delay if natural mortality is high, and the best yield is then obtained by harvesting small (young) animals (see Beverton and Holt, 1957; Ricker, 1958).

For high fishing mortalities (0.5 - 1.0), greatest yield per recruitment is obtained from the Banks Peninsula fishery when the minimum legal size is 110-120 mm if  $M = 0.05$ , or 110-110 mm if  $M = 0.1$ , 90-100 mm if  $M = 0.15$

Figure 7.7 Upper. Yield per recruitment isopleth diagram for the Peraki Bay population with the annual instantaneous natural mortality  $(M) = 0.05$ . Yields are in  $10^4$  g. per  $10^3$  two year old recruits.

Lower. The effect of exploitation on the expected number of spawning seasons to be experienced per two year old recruit (ES).  $M = 0.05$ .

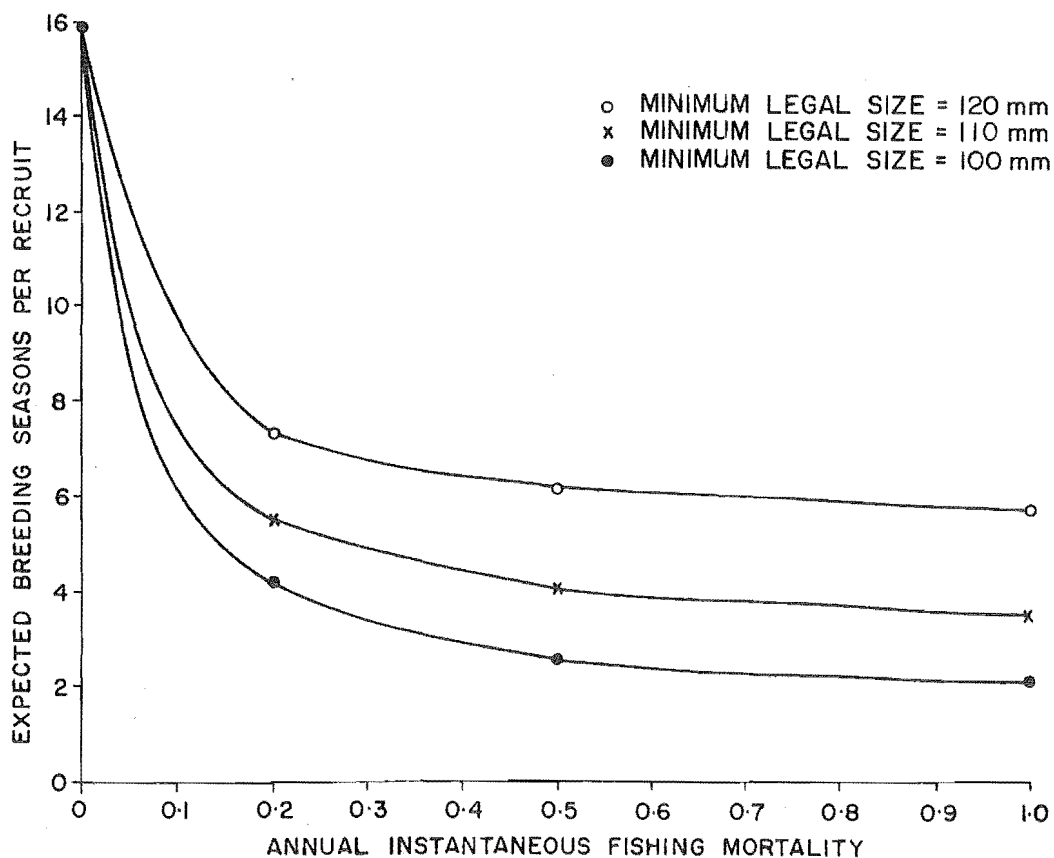
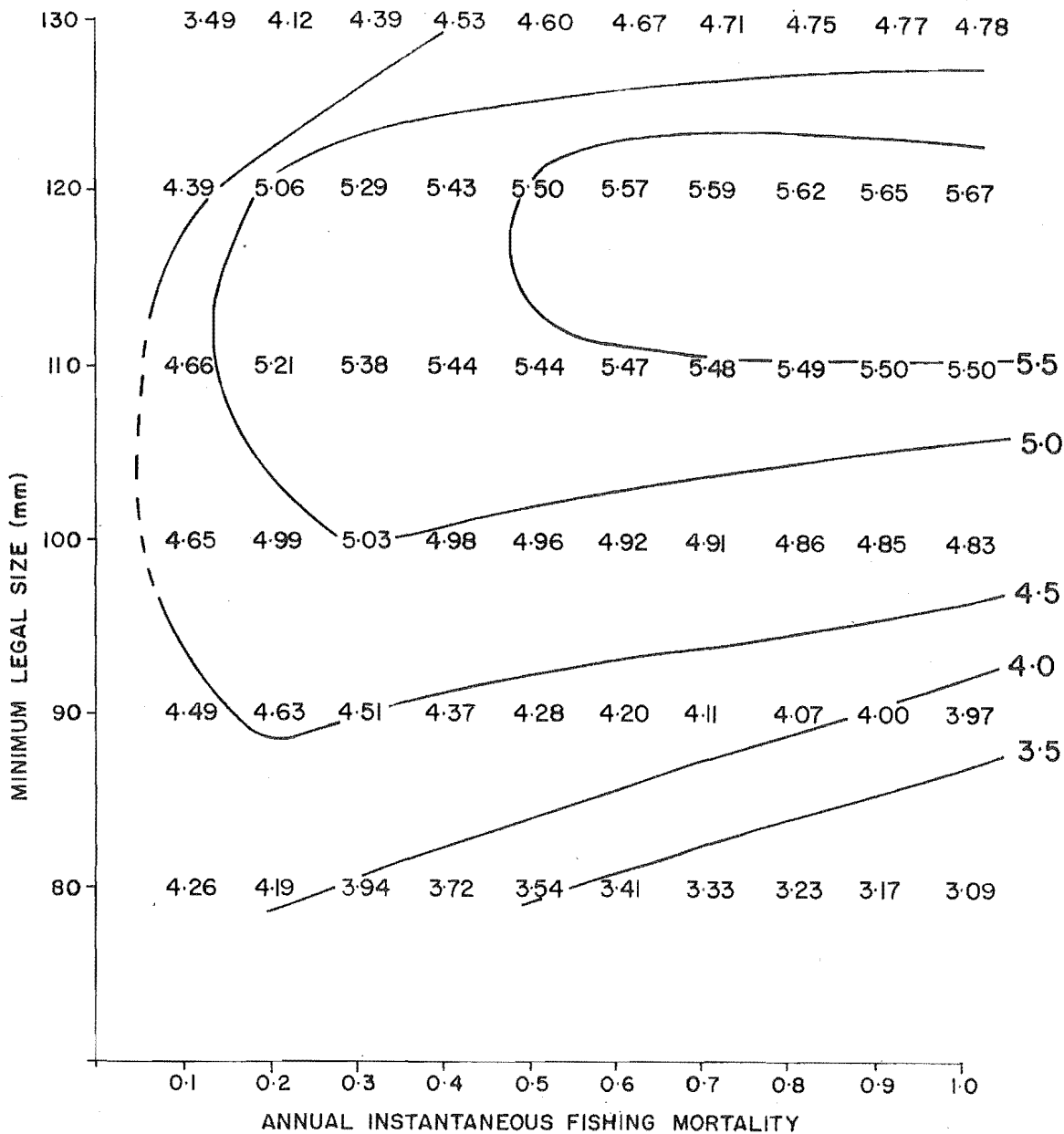


Figure 7.8 As for Figure 7.7 but with  $M = 0.1$ .



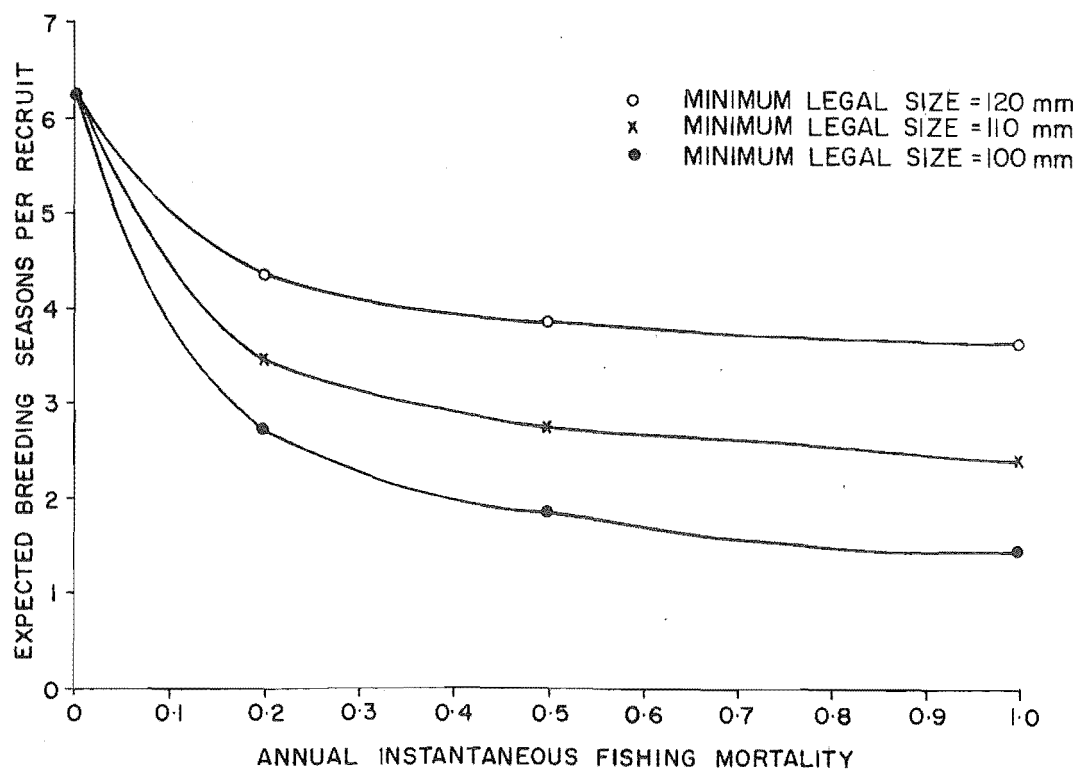
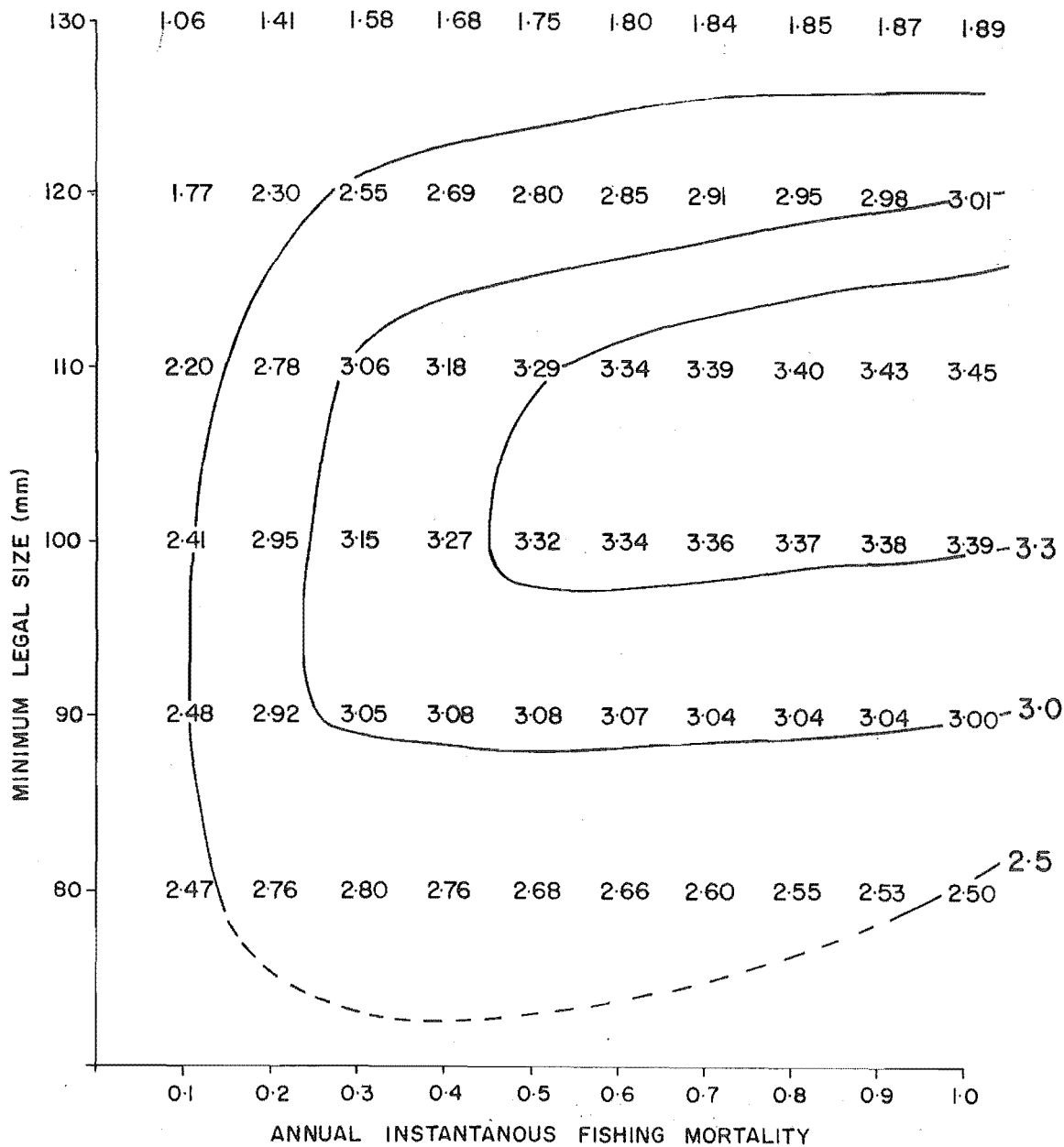


Figure 7.9 As for Figure 7.7 but with  $M = 0.15$ .

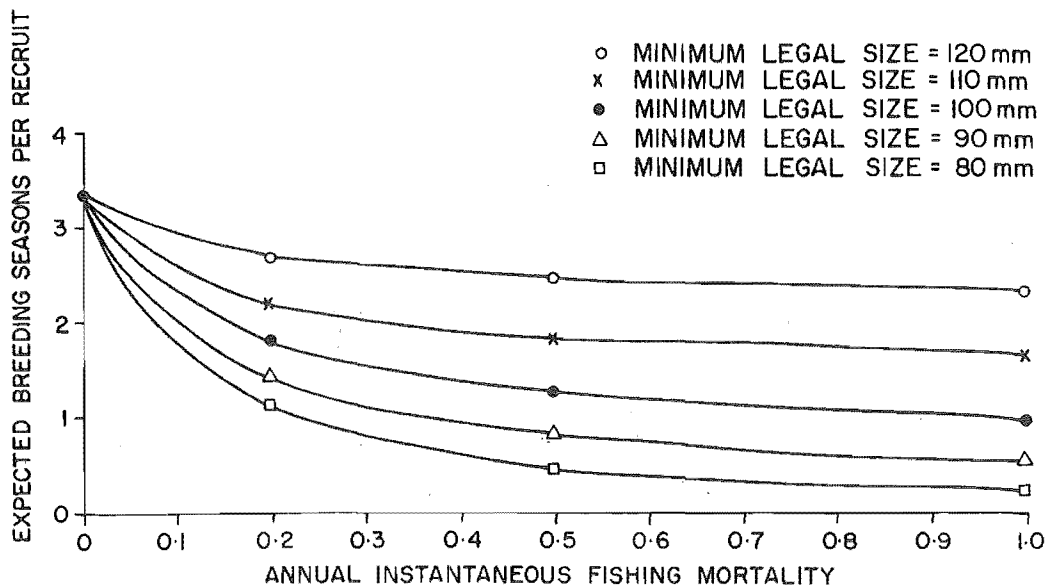
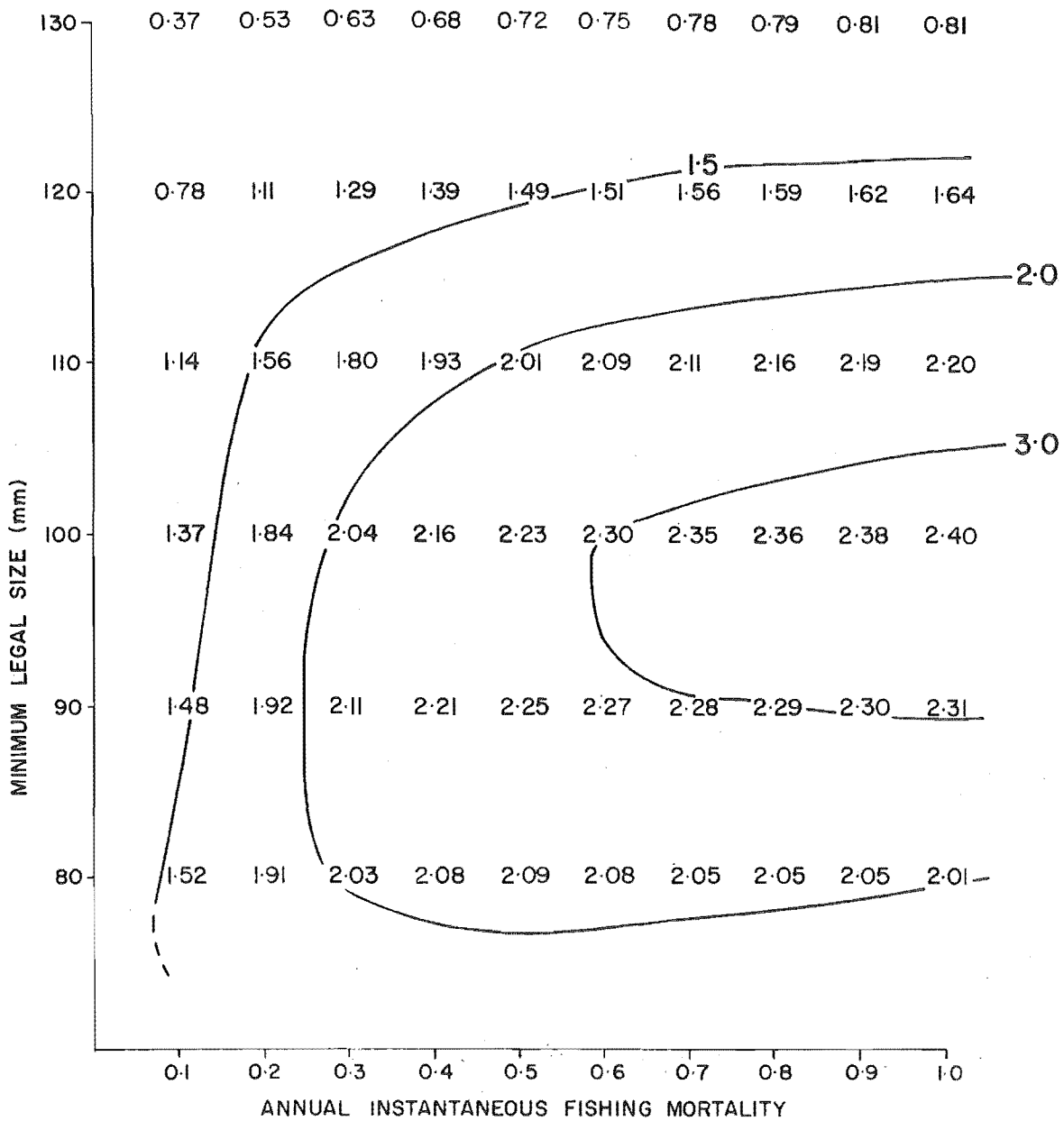
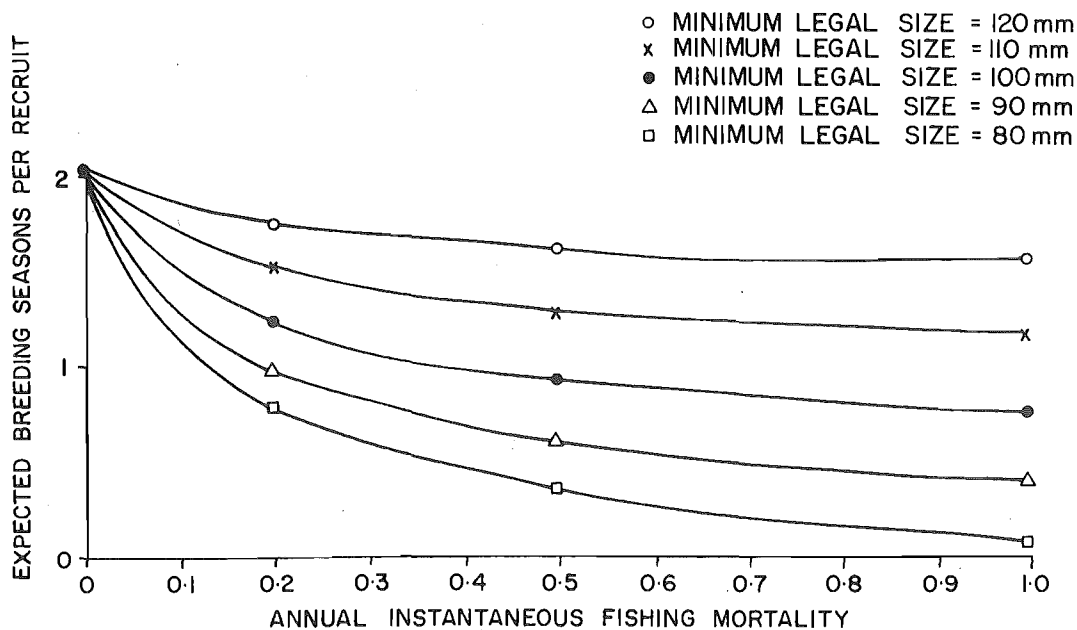
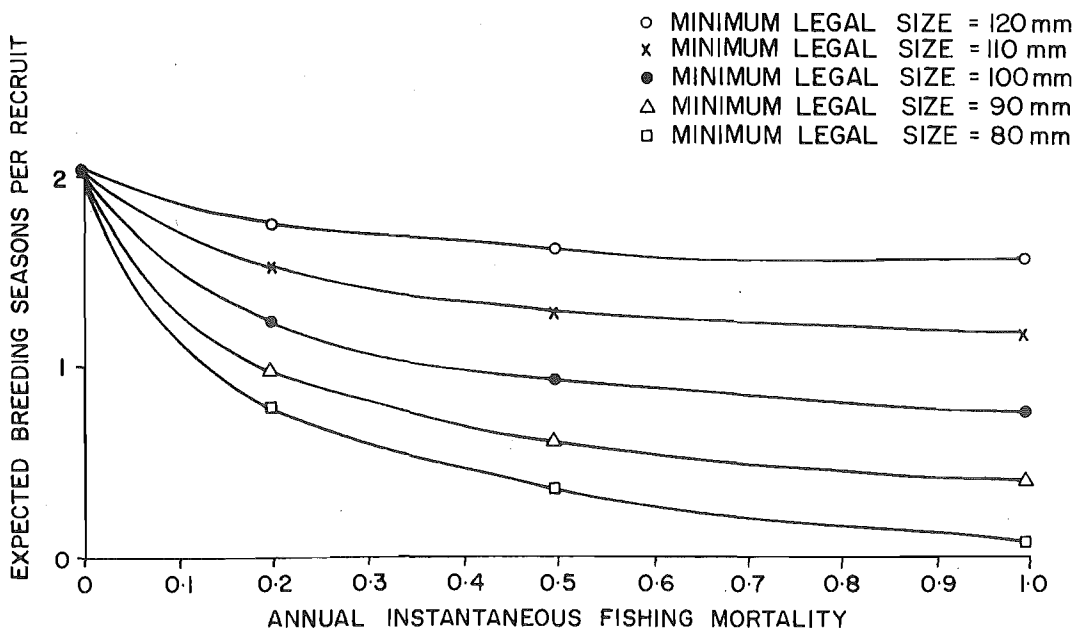


Figure 7.10 As for Figure 7.7 but with  $M = 0.2$ .



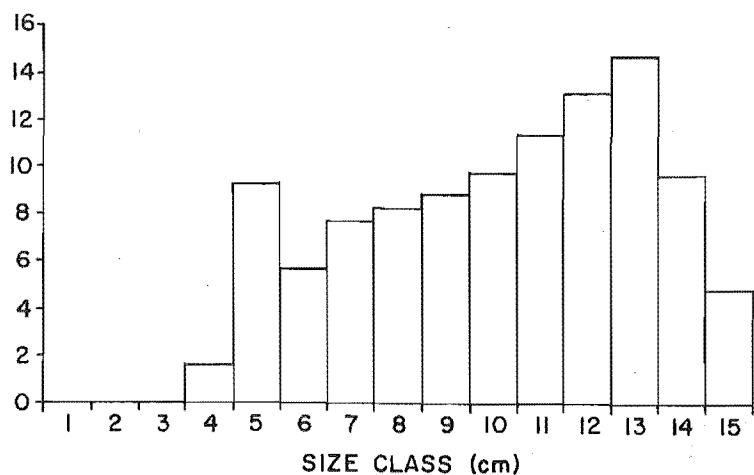
and 85-100 mm if  $M = 0.2$ . For low levels of exploitation the best minimum legal size remains about the same for  $M = 0.05 - 0.15$ , but if  $M = 0.2$  some benefit would be obtained from a slightly lower minimum legal size than should be used under a high fishing mortality.

The expected number of breeding seasons per recruit (ES) decreases rapidly from its natural (unfished) value with the imposition of even quite low fishing mortalities. A high fishing mortality applied with a minimum legal size of 110-120 mm to a population with  $M = 0.05$  results in ES values of 4-6 years, as compared with almost 16 years in the absence of fishing mortality. If  $M = 0.1$  and the stocks are intensively fished with a minimum legal size of 100-110 mm, the mean breeding life per recruit is reduced from the natural level of about 6 years to 1.5 - 2.5 years. The optimal minimum legal sizes suggested by the yield per recruitment analysis for natural mortalities of 0.15 - 0.2 result in a very low expected breeding life per recruit. If  $M = 0.15$  the expected breeding life is reduced from the unfished level of about 4 years to 0.8 - 1.5 years by fishing mortalities of 0.5 - 1.0. If  $M = 0.2$ , ES is reduced from about 2 years to 0.2 - 0.25 years.

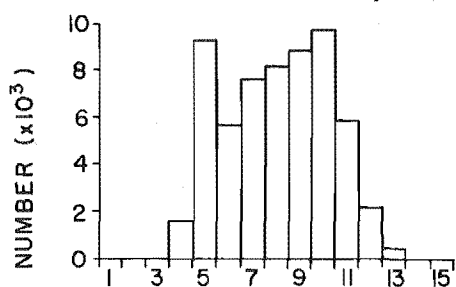
The size structure of the Banks Peninsula stock under equilibrium conditions for various regimes and  $M = 0.1$  is shown in Fig. 7.11. As would be expected, the effect of a fishery is to reduce the number of large individuals in the population, so reducing the skew to the left evident in the size structure of an unfished population under the same conditions of recruitment.

Figure 7.11 Equilibrium size structure per 1000 recruits of the Peraki Bay population under various fishing regimes and with  $M=0.1$ .  $F$  = annual instantaneous fishing mortality and M.L.S. = minimum legal size.

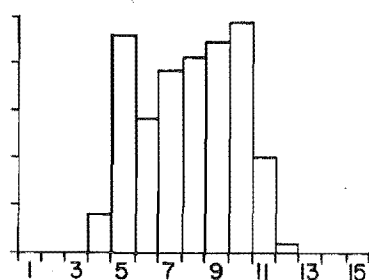
# FISHING MORTALITY (F) = 0.0



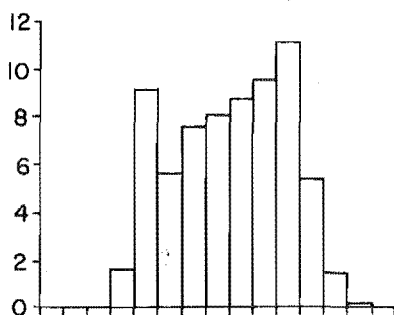
M.L.S. = 100 mm, F = 0.5



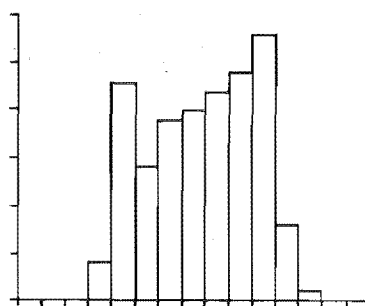
M.L.S. = 100 mm, F = 1.0



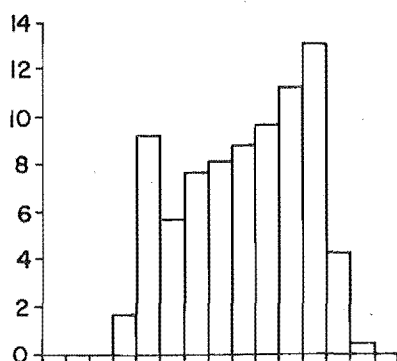
M.L.S. = 110 mm, F = 0.5



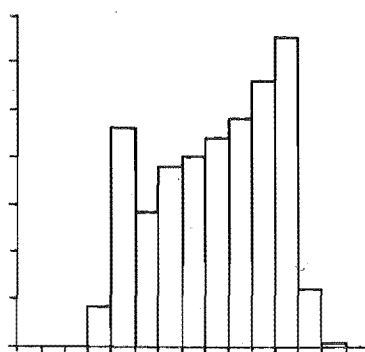
M.L.S. = 110 mm, F = 1.0



M.L.S. = 120 mm, F = 0.5



M.L.S. = 120 mm, F = 1.0





The degree of modification increases with increasing fishing mortality.

Yield per recruitment isopleth diagrams for the Kaikoura fishery and the effect of fishing mortality on the expected number of breeding seasons per recruit are given in Figs 7.12 and 7.13. If  $M=0.1$  and fishing mortality is high, the largest yield per recruitment is obtained using a minimum legal size at 115-135 mm. This results in a reduction of the average breeding life per recruit from the unfished level of 8.5 years to about 2 - 4.5 years. If  $M=0.2$  the highest yields result from a minimum legal size of about 105-115 mm, and the average breeding life is reduced from 3.5 years to about 2 years.

In comparing the magnitude of the yield per recruitment between Kaikoura and Banks Peninsula it must be remembered that the yields calculated for the Kaikoura population include the viscera, whereas those from Banks Peninsula are based on foot weight only (the foot is the most commercially valuable part of the abalone, and is therefore a better index of the value of the catch). For animals above about 100 mm the foot weight is about 70% of the foot plus viscera weight (Cleaver, 1966). Comparison of the yield per recruitment isopleth diagrams shows that the Kaikoura fishery must be regarded as more efficient than that at Banks Peninsula in terms of the maximum yield attainable per recruit, i.e. a greater yield could be obtained from a given recruitment at Kaikoura than would be possible from the same recruitment at Banks Peninsula.

Figure 7.12 Upper. Yield per recruitment isopleth diagram for the Kaikoura population with  $M = 0.1$ . Yields are in  $10^4$  g. per  $10^3$  two year old recruits.

Lower. The effect of exploitation on the expected number of spawning seasons to be experienced per two year old recruit (ES),  $M = 0.1$ .

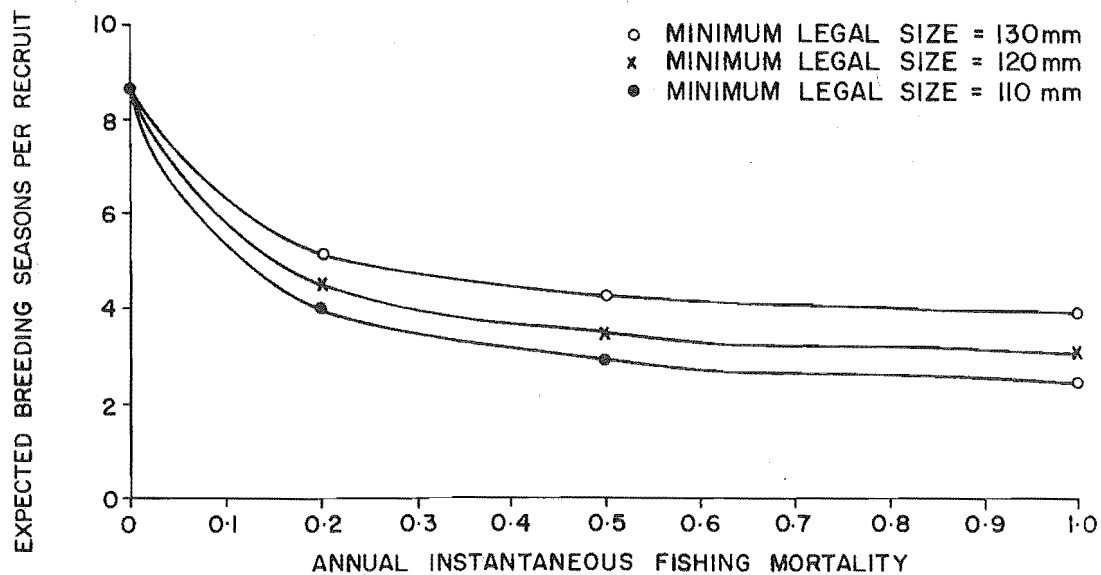
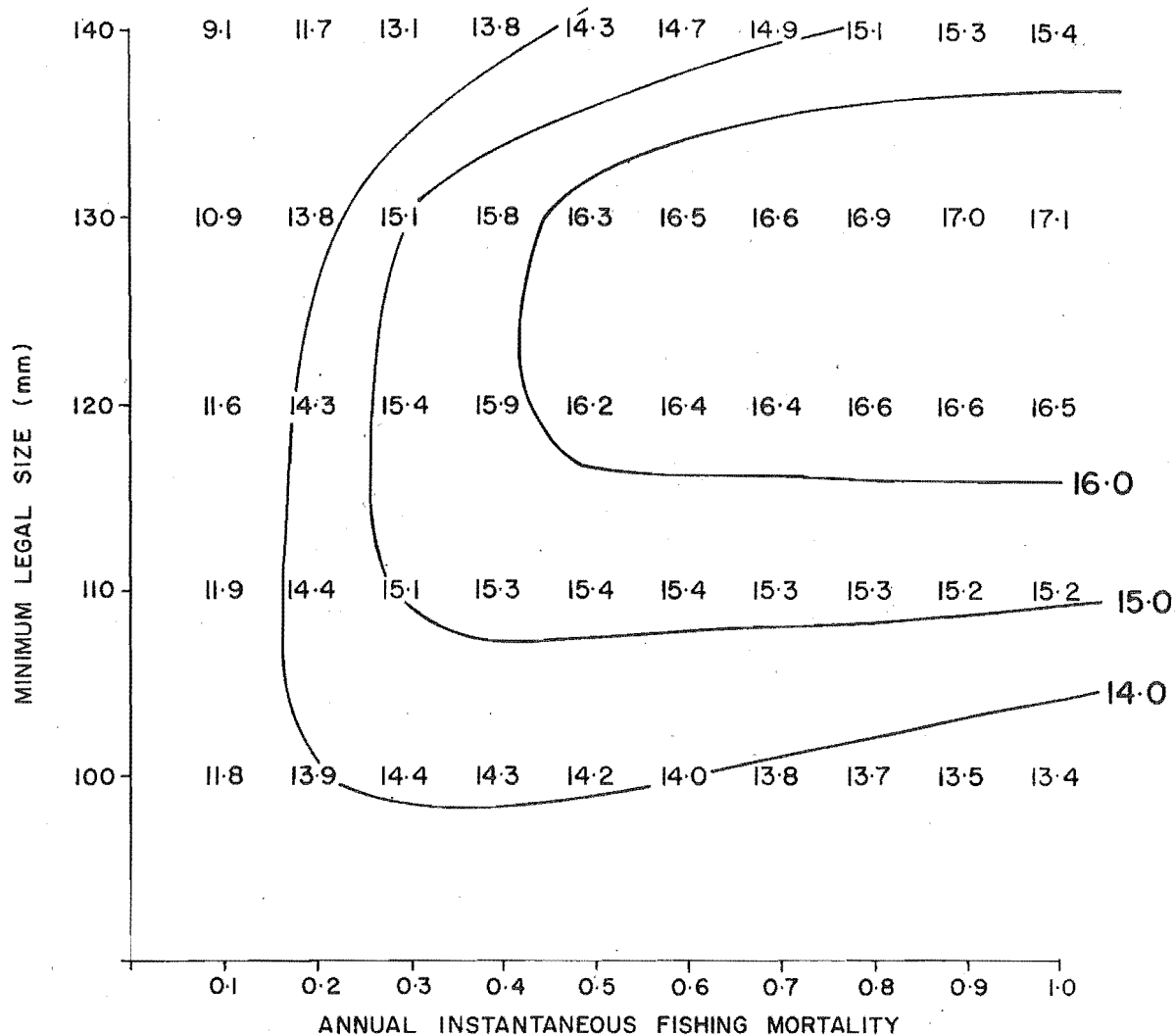


Figure 7.13 As for Figure 7.12 but with  $M=0.2$ .

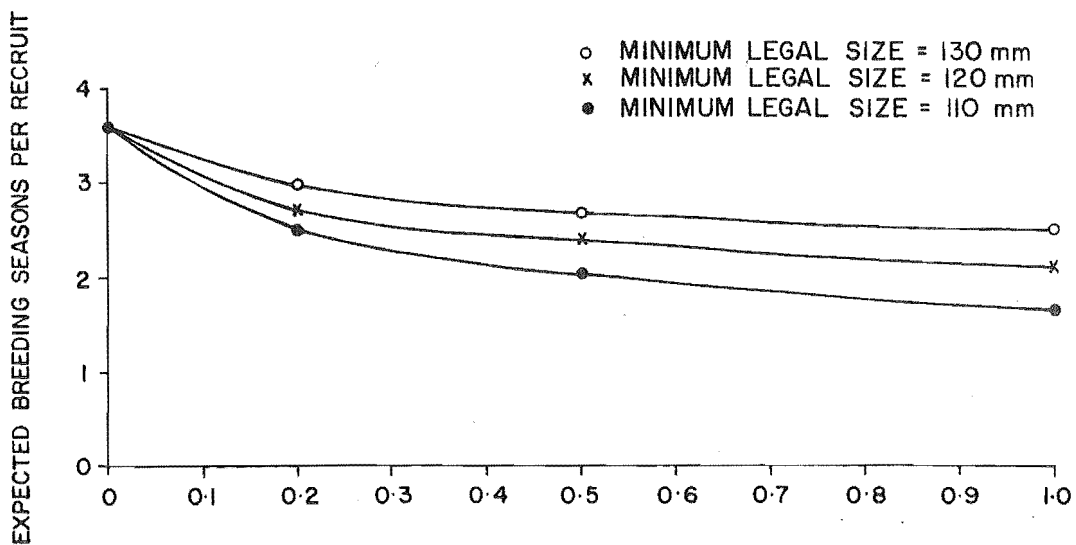
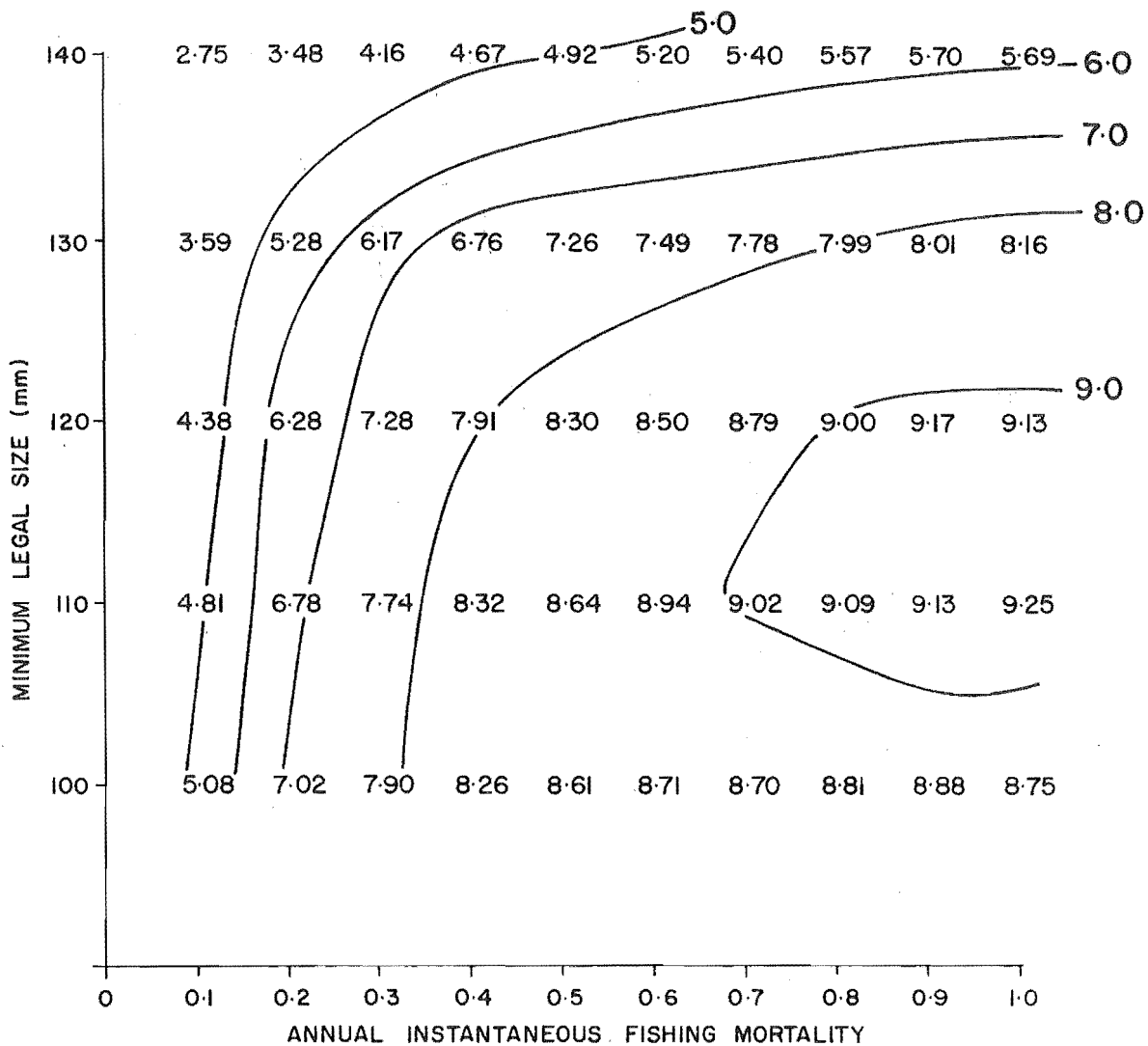
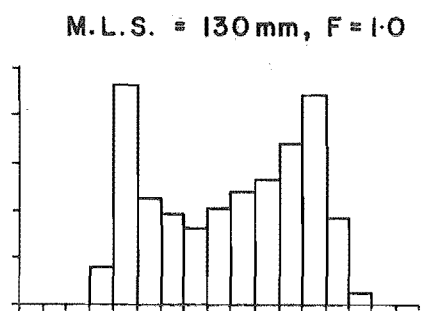
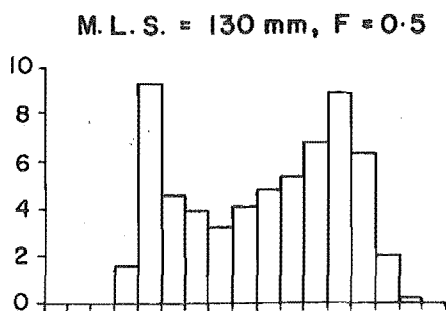
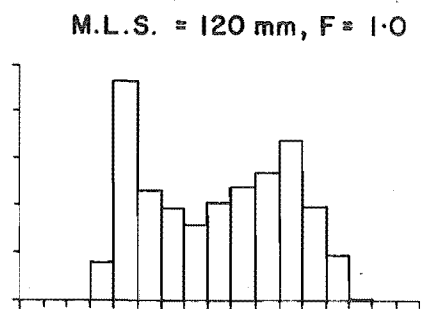
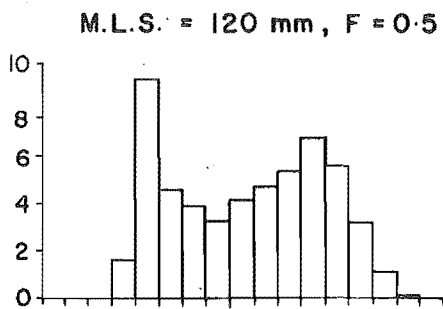
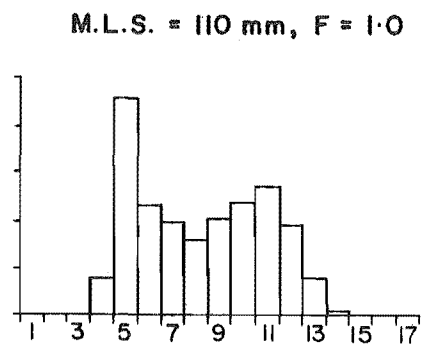
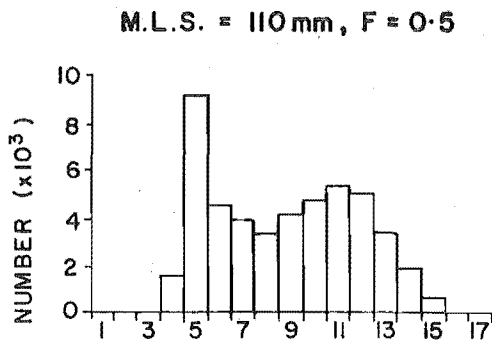
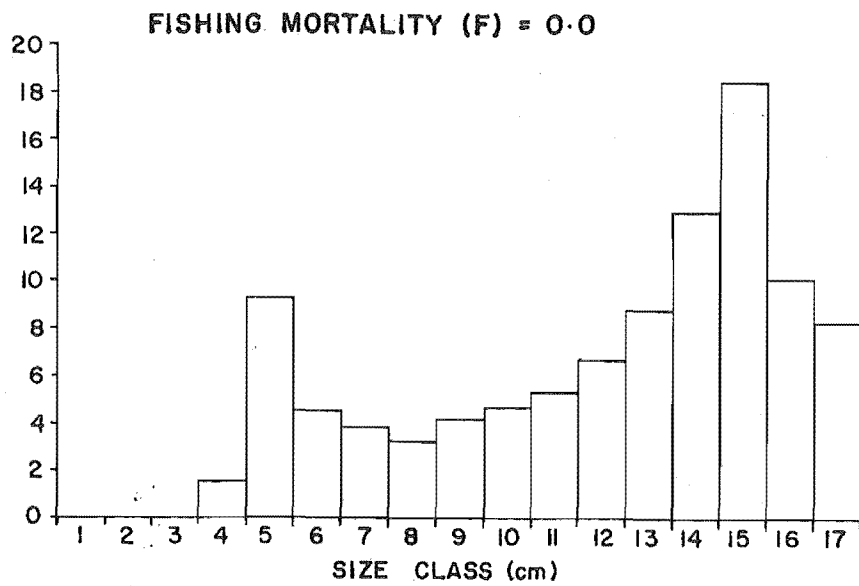


Figure 7.14    Equilibrium size structure, per thousand recruits, of the Kaikoura population under various fishing regimes and with  $M=0.1$ .

$F$  = Annual instantaneous fishing mortality and  
 $M.L.S.$  = minimum legal size.



The equilibrium size structure of the Kaikoura population under various fishing regimes is shown in Fig. 7.14.

#### 7.3.4 Discussion

The annual instantaneous natural mortality of *H. iris* on Banks Peninsula is probably about 0.1, and accordingly a minimum legal size of 100-110 mm would result in the largest yield per recruitment. Over the range of natural mortalities likely (0.1 - 0.2), the present minimum legal size of 127 mm should provide close to the maximum yield per recruitment for the Kaikoura fishery, although some increases of yield could be derived by decreasing the minimum legal size to 115 mm if natural mortality proves to be about 0.2.

The expected number of spawnings per recruit cannot be used to assess the 'sustainability' of the various fishing policies because a reduction of the mean breeding life per recruit does not in itself imply a given recruit is less likely to ultimately replace itself. The reduced breeding life would be associated with a reduced population density which may serve to increase individual fecundity (see Bagenal, 1973), while a reduction of the egg output of a population may result in an increase in egg to recruit survival (see Cushing and Harris, 1973; Larkin, 1973). Reduced population densities may also result in a decrease in the age at first reproduction. The combination of such responses may result in a sustainable fishery in which the expected number of eventual spawnings per recruit is well below that of an unfished population.



However, in view of the variable nature of recruitment (which may indicate that a strong density independent element exists in egg to recruit survival) and the failure of spawning in some years, fishing regimes which result in ES values of less than about 2-3 years must, for the present, be regarded as too severe. This limit is subjective, and may well be over-optimistic in the long term.

The problems of interpretation are further compounded by the possibility that recruitment to one area may be produced by stocks in some distant area, and that the fishing mortality in the two areas may be quite different. A case in point is the heavily exploited Kaikoura population which may receive the bulk of its recruitment from the largely unfished stocks between the Waipara River and Hamuri Bluff. Under such conditions the magnitude and pattern of recruitment to Kaikoura would be little affected by whatever local fishing pressure was applied, and would remain much the same as it was before exploitation began. The effect of fishing on the egg production of the Kaikoura population may be apparent only in the recruitment to stocks further north. Similarly, the recruitment to Banks Peninsula may be affected in future years by recent exploitation of the Oamaru stocks. Assuming the recruitment to Kaikoura is not as variable as that to Peraki Bay, it would be possible for the Kaikoura fishery to stabilise (i.e. catch and catch per unit effort remain relatively constant over a long period) under the level of recruitment provided by the unfished stocks to the south. No matter how long these

stable conditions persisted, they could not be taken as evidence for the long-term 'sustainability' of the particular fishing regime if it were applied over a more widespread area (i.e. to include the parent stock). The nature of the Kaikoura fishery could change rapidly (not necessarily for the worse) if stocks between the Waipara River and Hamuri Bluff were exposed to an increased fishing mortality.

## GENERAL CONCLUSIONS

The two main aims of this study were

- i) to examine the dynamics of the Peraki Bay *H. iris* population, and
- ii) to use the insights and estimates obtained from this population for the evaluation of various fishing strategies.

In section 7.2 the population parameters of *H. iris* from Peraki Bay are fully summarised and compared with those of *H. iris* from Kaikoura. This comparison reveals that the Peraki Bay population is not living under optimal conditions for the species. It is poorly positioned geographically to receive recruitment via the dominant current system in the area, and is probably very dependent on rare combinations of events which result in occasional years of very heavy settlement of larvae. Having settled, the abalone on Banks Peninsula are subject to high silt loads in the water and the danger of burial by sediment. The individual growth rate and maximum size of *H. iris* on Banks Peninsula are low as compared to those found in other areas, probably as a result of a poor food supply.

To obtain the maximum yield per recruit, the minimum legal size for Banks Peninsula should be reduced to 100-110 mm. However, the desirability of such a reduction is highly questionable. If the minimum legal size on Banks Peninsula were lower than that in force elsewhere in the

country, efforts would have to be made to ensure that animals harvested in other localities were not transported to Banks Peninsula and 'landed' there. Enforcement would probably require an increase in the number and mobility of fisheries' inspectors on Banks Peninsula. Furthermore, the variable nature of recruitment makes it unlikely that an intensive fishery could be supported on Banks Peninsula on a permanent basis. If there are 10-15 year periods of low recruitment between shorter periods of high recruitment, sufficient stocks for the fishery may only exist for a few years as the pulse of good recruitment is harvested. Following this, fishermen would have to find alternative stocks or employment until the next pulse of good recruitment becomes fishable. This situation could be improved by the creation of a limited licence fishery in which few fishermen were allowed to operate on Banks Peninsula. Such legislation could be used to maintain the fishing mortality at a level which left the stocks at commercial densities between pulses of good recruitment (although it would also reduce the yield per recruitment). Unfortunately, the data necessary for the management of such a fishery are not available (notably the total size of the Banks Peninsula stock, the long-term recruitment pattern and the relationship between fishing effort and fishing mortality). Thus, with the present state of knowledge, the current minimum legal size should probably be retained for Banks Peninsula. For high fishing mortalities the yield per recruit expected using the existing minimum legal size of 127 mm is 50-55% of the maximum possible, and so if this

size limit is retained steps should be taken to promote greater access to large individuals in the stock than is possible under present legislation. Most large abalone on Banks Peninsula are found on the exposed headlands at depths of 8-15 m where, with the extremely low underwater visibilities typical of the region, they are difficult for a snorkel diver to collect. Thus good yields are unlikely to be obtained unless fishermen on Banks Peninsula are permitted to use underwater breathing apparatus.

Analysis of the Kaikoura fishery was made assuming that natural mortality was similar to that at Peraki Bay (i.e. between 0.1 and 0.2), and so must be regarded as tentative. Over this range of natural mortality, however, the yield per recruit using the present minimum legal size is close the maximum possible for a wide range of fishing mortalities. If future work establishes that the natural mortality is about 0.2, a 6-12% increase in the yield per recruit could be expected from a decrease of the minimum legal size to 115 mm.

Reasonable conclusions concerning the long-term 'sustainability' of the fishery require a far greater knowledge of larval transport and egg to recruit survival than is presently available. However, since abalone under natural conditions have a long reproductive life and the populations have a huge egg output due to accumulated old individuals, it may be inferred that they are well able to withstand prolonged periods of extremely low egg-to-recruit survival, and that such periods (although perhaps rare) may be very important aspects of the population dynamics of the

species. Excessive reduction of the expected reproductive life by fishing may reduce the resilience of populations to such occurrences, despite possible compensatory changes in larval and pre-recruit survival. This could be especially important if exploitation becomes intense over a wide geographical area. If population densities are severely reduced, there is also a possibility that the sea urchin *Evechinus chloroticus* may invade and modify the abalone habitat to such an extent that the abalone are subsequently excluded (see Shepherd, 1973b). For these reasons it is important that a continuing programme of research be devised to monitor recruitment to a few representative populations (perhaps at Wellington, Kaikoura and Stewart Island). The time commitment should not be excessive as juveniles in many areas can be sampled intertidally. The information obtained could be used both to provide an early warning of prolonged recruitment failure and to investigate the long-term pattern of recruitment.

The present knowledge of the population dynamics of *H. iris* is limited in both depth and scope. Considerable differences in the population parameters of the Kaikoura and Peraki Bay populations suggest that intensive work may be necessary in several localities before the nationwide fishery can be managed to best advantage. The most urgent topics for future research on *H. iris* include larval transport, egg-to-recruit survival, the temporal pattern of recruitment, and the size specific mortality rate. Data concerning the planktonic stage are likely to be

extremely difficult to collect, but reliable estimates of mortality could be obtained from large scale tagging experiments such as those undertaken in Australia (Beinssen and Powell, 1976).

Although the size class population model is not field tested, it provides intuitively reasonable estimates of natural mortality, yield per recruitment and the historical pattern of recruitment for the Peraki Bay abalone population. Potentially the model is a useful tool for examining the population dynamics and exploitation of species which cannot be aged, and the model warrants critical evaluation and further development. Insufficient time was available to both evaluate the population model and conduct the Peraki Bay field programme, and as this study was commissioned to examine the population dynamics of *H. iris*, priority had to be given to the field programme. Most effort for the future development of the model will probably centre on the treatment of the growth process. The treatment of growth provided here must be regarded as a 'first analysis' which, although probably adequate, is in many ways deficient and would benefit from further examination. Whatever future modifications are made to the treatment of growth, it is desirable that estimates of the parameters of the equations be obtainable from tag return data (rather than laboratory studies) because for many species field tagging experiments provide the only readily accessible source of information on growth.

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## APPENDIX 1.1

We want to predict the growth in length, during the time interval  $t$ , of the individuals initially in source size class  $j$ . For each animal ( $m$ )

$$l_{m,T+t} = l_{m,T} + I_{m,t} \quad (i)$$

where the growth increment ( $I_{m,t}$ ) is some function of initial length and is subject to individual variation.

The expected value of  $l_{T+t}$  for a group of animals is

$$\begin{aligned} E[l_{m,T+t}] &= E[l_{m,T} + I_{m,t}] \\ &= E[l_{m,T}] + E[I_{m,t}] \end{aligned} \quad (ii)$$

and the variance is

$$V[l_{m,T+t}] = V[l_{m,T}] + V[I_{m,t}] + 2 \text{Cov}[l_{m,T}, I_{m,t}] \quad (iii)$$

If the size classes are small, the distribution of lengths within each size class is approximately uniform, giving

$$E[l_{m,T}] = \hat{l}_j$$

and

$$V[l_{m,T}] = h_j/12$$

where  $\hat{l}_j$  is the mid point and  $h_j$  is the width of the  $j$ th size class. To obtain expressions for  $E[I_{m,t}]$ ,  $V[I_{m,t}]$  and  $\text{cov}[l_{m,T}, I_{m,t}]$  we must specify the form of the growth function relating the growth increment to initial length

and the period of growth ( $t$ ). Here the Von Bertalanffy relationship will be used. This growth equation was derived by considering the growth of an animal to be due to the differences between anabolic and catabolic processes of an animal's metabolism (see Von Bertalanffy, 1938; Fabens, 1965; Ursin, 1967). We may consider a number of such animals, each with its own pair of Von Bertalanffy growth constants ( $L_m, K_m$ ) which it retains throughout life. Thus, if the whole population were examined, a frequency distribution could be formed for  $L$  and  $K$  from which a mean and variance could be calculated. It is assumed here that the values of  $L_m$  and  $K_m$  possessed by an animal are independent, and that for the population  $V[L_m]$  and  $V[K_m]$  are independent of length. Neither of these assumptions is likely to be strictly true, but the error involved is probably small. (Equations analogous to those given here could be developed without making these assumptions, however they become very complex and the parameters of the resulting growth equation would be very difficult to estimate.) For an animal of initial length  $l_{m,T}$ , the growth increment  $I_{m,t}$  during time  $t$  is

$$I_{m,t} = (L_m - l_{m,T}) (1 - e^{-K_m t})$$

For a group of animals we first note that

$$E[I/l, t] = (E[L_m] - l) (1 - E[e^{-K_m t}]) \quad (\text{iv})$$

and

$$\begin{aligned}
 V[I/l, t] &= E[I^2/l, t] - E[I/l, t]^2 \\
 &= V[L_m] \{V[e^{-K_m t}] + (1 - E[e^{-K_m t}])^2\} \\
 &\quad + V[e^{-K_m t}] (E[L_m] - 1)^2
 \end{aligned} \tag{v}$$

For the animals originally in class  $j$

$$\begin{aligned}
 E[I_{m, t}] &= E[(L_m - l_m) (1 - e^{-K_m t})] \\
 &= (E[L_m] - E[l_m]) (1 - E[e^{-K_m t}])
 \end{aligned}$$

Thus if the initial distribution of lengths within  $j$  is uniform, we have from (ii) and (iv)

$$\begin{aligned}
 E[l_{m, T+t}] &= \hat{l}_j + (E[L_m] - \hat{l}_j) (1 - E[e^{-K_m t}]) \\
 &= E[L_m] (1 - E[e^{-K_m t}]) + E[e^{-K_m t}] \hat{l}_j
 \end{aligned} \tag{vi}$$

To obtain the variance  $V[I_{m, T+t}]$  from (iii) we must evaluate  $V[I_{m, t}]$  and  $\text{Cov}[l_{m, T}, I_{m, t}]$ .

$$\begin{aligned}
 V[I_{m, t}] &= E[I_{m, t}^2] - E[I_{m, t}]^2 \\
 &= V[L_m] \{V[e^{-K_m t}] + (1 - E[e^{-K_m t}])^2\} \\
 &\quad + V[e^{-K_m t}] (E[L_m] - E[l_{m, T}])^2 + V[l_{m, T}] V[e^{-K_m t}] \\
 &\quad + V[l_{m, T}] (1 - E[e^{-K_m t}])^2
 \end{aligned}$$

putting  $E[l_{m, T}] = \hat{l}$  for ease of notation

$$V[I_{m, t}] = V[I/\hat{l}, t] + V[\hat{l}_{m, T}] V[e^{-K_m t}] + V[l_{m, T}] (1 - E[e^{-K_m t}])^2$$

$$\begin{aligned} \text{and } \text{Cov}[l_{m,T}, I_{m,t}] &= E[(l_m - E[l_{m,T}]) (I_m - E[I_m])] \\ &= -V[l_{m,T}] (1 - E[e^{-K_m t}]) \end{aligned}$$

And so from (iii)

$$\begin{aligned} V[l_{m,T+t}] &= V[l_{m,T}] + V[I_{m,t}] + 2 \text{Cov}[l_{m,T}, I_{m,t}] \\ &= V[l_{m,T}] + V[I_m/l, t] + V[l_{m,T}] V[e^{-K_m t}] \\ &\quad + V[l_{m,T}] (1 - E[e^{-K_m t}])^2 - 2 V[l_{m,T}] (1 - E[e^{-K_m t}]) \\ &= V[I_m/\hat{l}, t] + V[l_{m,T}] \{V[e^{-K_m t}] + E[e^{-K_m t}]^2\} \end{aligned}$$

which, if the initial distribution is uniform, gives

$$V[l_{m,T+t}] = V[I/\hat{l}_j, t] + \frac{h_j^2}{12} (E[e^{-K_m t}]^2 + V[e^{-K_m t}]) \quad (\text{vii})$$

Thus equations (vi) and (vii) define the mean and variance of length at time  $T+t$  of the group of animals in size class  $j$  at time  $T$ . The relationship  $V[I/\hat{l}_j, t]$  is defined by equation V, and the parameters  $E[L_m]$ ,  $V[L_m]$ ,  $E[e^{-K_m t}]$  and  $V[e^{-K_m t}]$  are obtained from the analysis of tag return data (further discussed in Appendices 3.2 and 3.3).



## APPENDIX 1.2

Certain generalisations may be made about the solutions of

$$\tilde{A} \tilde{V} = \lambda \tilde{V} \quad (i)$$

where  $A$  is an age or size class projection matrix. From the Perron-Frobenius theorem (Gantmacher, 1959; Franklin, 1968), if a matrix of order  $z$  has no negative elements and is irreducible, then only one of the  $z$  eigenvalues, that of greatest modulus, has a corresponding eigenvector consisting of all non-negative elements. This is the dominant eigenvalue, which, with its associated eigenvector, provides the only biologically acceptable solution of (i). Bounds for the dominant eigenvalue ( $\lambda_1$ ) may be obtained directly from the projection matrix since it can be shown (lucidly by Vanga, 1962) that the modulus of  $\lambda_1$  is greater than the minimum row sum and less than the maximum row sum (where all row sums are not equal), or equals a row sum (when all row sums are equal).

Irreducibility for a matrix  $A$  of order  $z$  is defined by Franklin as "... for all pairs of indices,  $p \neq q$ , either  $a_{p,q} \neq 0$  or there is some set of indices,  $i_1 \dots i_r$  which are all different ( $r < z - 2$ ) such that

$$a_{p,i_1} \neq 0, a_{i_1,i_2} \neq 0, \dots a_{i_{r-1},i_r} \neq 0 \text{ and } a_{i_r,q} \neq 0 \dots"$$

A sufficient condition for irreducibility then is that each row and each column has a non-zero element somewhere other than on the principle diagonal and that  $a_{1,z}$  is non-zero. For  $a_{1,z}$  to be non-zero in the projection matrix the oldest or largest class of the population must not consist entirely of post-reproductives. If a population contains such classes, they must be excluded for the solution of (i) by removal of the relevant row and column of the projection matrix, so reducing its order.

A row of zero elements in either the age or size class matrix means that a class exists which, with the interval  $t$  used, can never contain animals. For a column of zeros, a class exists which in no way contributes to the population structure at  $T+t$ . In either case the class concerned is excluded from the analysis and the relevant row and column removed from the matrix. These conditions simply eliminate any class which does not influence the population growth rate, and once they are removed, the resulting projection matrix (of order  $\leq z$ ) will yield only one meaningful solution to equation (i).

While it is quite possible that any projection matrix may require these modifications before it is solved for its dominant eigenvalue, the conditions are most likely to arise when seasonal matrices are pre-multiplied to give one annual projection matrix using equation (10).

For example, if a species breeds seasonally some seasonal matrices will contain fecundity terms equal to zero, so certain rows of the resulting annual projection matrix may be made up of zero elements.

The conditions and methods outlined above are only relevant when a matrix is being solved for its dominant eigenvalue and associated eigenvector. There are no such restrictions on the projection matrix if it is being used iteratively. Also, if a matrix is reduced in order by the elimination of one or more classes, the behaviour of these classes at stability may still be investigated.

If projection matrix  $A$  has certain rows and columns removed, in accordance with the above discussion, to give matrix  $A'$  which is solved for  $\lambda'_1$  and  $\tilde{V}'$ , then  $\lambda'_1 = \lambda_1$  and  $\tilde{V}'$  is found by iterating

$$\tilde{V}' = A' \tilde{V}'$$

beginning with  $v_i = v'_i$  if class  $i$  is in  $A'$

$$v_i = 0 \quad \text{otherwise}$$

until the elements of  $\tilde{V}'$  occur in constant proportions.

## APPENDIX 2.1

Summary of the results of the 1974 transect sampling.  
Each column represents a transect.

S T R A T U M																				
Size (mm)	EI						EJ							WJ						
							*	*	*	*	*	*	*	*	*	*	*	*	*	*
0 - 10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 - 20	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
21 - 30	1	0	0	2	1	0	1	0	0	0	2	0	1		0	0	0	0	0	0
31 - 40	3	1	1	2	2	0	0	1	1	3	0	1	2		0	3	1	3	1	0
41 - 50	1	0	1	7	3	0	1	1	1	4	5	3	1		0	2	1	3	3	0
51 - 60	1	0	1	3	7	2	0	0	1	0	0	0	0		0	0	1	0	0	0
61 - 70	2	2	0	2	5	3	2	3	3	3	2	2	2		4	1	2	2	1	4
71 - 80	0	8	3	6	4	5														
81 - 90	1	5	4	2	4	5														
91 - 100	3	3	16	5	8	7														
101 - 110	7	13	17	9	8	23														
111 - 120	5	16	16	11	17	25														
121 - 130	2	5	0	3	2	6														
Total	27	53	59	52	61	76														

\* Juvenile-only transects

Summary of the results of the February 1976 transect sampling.  
Each column represents a transect.

S T R A T U M																					
Size (mm)	EA			WA		EI			WI			EJ							WJ		
																*	*	*	*	*	
0 - 10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
11 - 20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
21 - 30	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	
31 - 40	0	0	0	0	0	3	0	0	0	0	0	1	0	3	1	1	0	1	0	0	
41 - 50	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	3	0	4	5	
51 - 60	0	0	0	0	0	0	0	2	0	0	0	0	1	1	1	3	3	3	4	5	
61 - 70	1	0	1	0	0	1	0	3	0	1	0	4	2	4	2	4	1	0	0	2	
71 - 80	0	1	2	0	0	2	0	2	1	3	1	3	6	8	5	7					
81 - 90	0	0	13	0	0	4	1	4	2	1	1	4	4	3	3	4					
91 - 100	5	0	25	0	0	11	12	4	1	3	4	9	4	6	0	7					
101 - 110	13	7	32	0	2	19	18	12	3	13	11	10	4	9	8	7					
111 - 120	28	11	20	4	8	13	15	16	7	10	6	10	8	3	4	2					
121 - 130	13	1	1	11	16	5	1	2	3	3	0	1	0	1	0	0					
131 - 140	3	1	0	7	2	0	0	0	1	0	0	0	0	0	0	0					
Total	63	21	94	22	28	58	47	46	18	34	23	42	29	40	24	36					

\*Juvenile-only transects

Summary of the results of the December 1976 transect sampling. Each column represents a transect.

Size (mm)	Stratum EI			
0 - 10	0	0	0	0
11 - 20	0	0	0	0
21 - 30	0	0	0	0
31 - 40	0	0	0	0
41 - 50	1	0	0	1
51 - 60	1	0	0	0
61 - 70	2	0	1	0
71 - 80	1	1	0	1
81 - 90	4	2	2	1
91 - 100	14	9	8	5
101 - 110	31	12	19	11
111 - 120	18	13	15	7
121 - 130	6	3	2	1
131 - 140	1	0	0	0
Total	79	40	47	27

## APPENDIX 3.1

Data obtained from tagging experiments at Peraki Bay.  
 The generally accepted seasons in New Zealand are  
 summer, December-February; autumn, March-May;  
 winter, June-August; spring, September-November.

Initial length (mm)	Growth increment (mm)	Time at liberty (yrs)	Period
105	3	0.1507	Feb - Apr
106	1	0.1507	Feb - Apr
113	7	0.1507	Feb - Apr
113	9	0.8164	Feb - Dec
120	2	0.6657	Apr - Dec
99	3	0.1507	Feb - Apr
99	3	0.8164	Feb - Dec
102	0	0.6657	Apr - Dec
106	2	0.1507	Feb - Apr
109	0	0.1507	Feb - Apr
112	2	0.1507	Feb - Apr
110	0	0.1507	Feb - Apr
118	0	0.1507	Feb - Apr
118	0	0.8614	Feb - Dec
118	0	0.6657	Apr - Dec
116	0	1.0219	Nov - Dec
122	2	0.8164	Feb - Dec
110	5	0.8164	Feb - Dec
107	1	0.8164	Feb - Dec
106	0	0.8164	Feb - Dec
117	0	0.8164	Feb - Dec
128	0	0.8164	Feb - Dec

Initial length (mm)	Growth increment (mm)	Time at liberty (yrs)	Period
115	0	0.8164	Feb - Dec
117	0	0.8164	Feb - Dec
124	1	0.8164	Feb - Dec
98	2	0.8164	Feb - Dec
115	0	0.1808	Nov - Feb
115	3	0.3014	Nov - Mar
115	3	0.1205	Feb - Mar
112	0	0.1808	Nov - Feb
110	4	0.1808	Nov - Feb
110	5	0.3014	Nov - Mar
114	1	0.1250	Feb - Mar
116	0	0.0959	Feb - Mar
116	0	0.0959	Feb - Mar
116	0	0.0959	Feb - Mar
112	1	0.0959	Feb - Mar
69	6	0.0959	Feb - Mar
69	11	0.8164	Feb - Dec
75	5	0.6959	Mar - Dec
110	0	0.0959	Feb - Mar
114	5	0.0959	Feb - Mar
125	1	0.1507	Feb - Apr
99	3	0.1507	Feb - Apr
91	9	0.3562	Nov - Apr
125	1	0.1507	Feb - Apr
78	4	0.1507	Feb - Apr
119	0	0.1507	Feb - Apr
95	4	0.1507	Feb - Apr



Initial length (mm)	Growth increment (mm)	Time at liberty (yrs)	Period
102	3	0.1507	Feb - Apr
106	2	0.1507	Feb - Apr
78	1	0.1507	Feb - Apr
78	5	0.8164	Feb - Dec
79	4	0.6657	Apr - Dec
113	1	0.1507	Feb - Apr
113	2	0.1507	Feb - Apr
102	4	1.0219	Nov - Dec
105	3	0.8164	Feb - Dec
111	6	0.8164	Feb - Dec
74	15	0.8164	Feb - Dec
87	10	0.8164	Feb - Dec
109	0	0.8164	Feb - Dec
92	6	1.1014	Nov - Jan
103	0	1.1014	Nov - Jan
116	3	1.1014	Nov - Jan
106	7	0.8959	Feb - Jan
115	2	0.8959	Feb - Jan
109	6	0.8959	Feb - Jan
105	3	0.8959	Feb - Jan
109	5	0.8959	Feb - Jan
110	7	0.8959	Feb - Jan
75	3	0.8959	Feb - Jan
95	4	0.8959	Feb - Jan
101	3	0.8959	Feb - Jan
118	0	0.8000	Feb - Jan
114	6	0.8959	Feb - Jan
119	1	0.8959	Mar - Jan

## APPENDIX 3.2

As outlined in Appendix 1.1, a population may be considered to consist of individuals each growing according to the Von Bertalanffy equation and possessing a specific pair of Von Bertalanffy growth constants ( $L_i$ ,  $K_i$ ) which are retained throughout life. It is assumed that  $L_i$  and  $K_i$  are independent. There is a population mean and variance for each parameter, and these are assumed to be constant over the length range of the species.

For an animal of initial length  $l_i$ , the growth increment ( $I_i$ ) during time interval  $t_i$  is

$$I_i = (L_i - l_i) (1 - e^{-K_i t_i})$$

and, as shown in Appendix 1.1, for a group of animals

$$E(I/l, t) = (E[L_i] - l) (1 - E(e^{-K_i t})) \quad i)$$

and

$$V(I/l, t) = k_1 V[L_i] + k_2 (E[L_i] - l)^2 \quad ii)$$

$$\text{where} \quad k_1 = 1 - 2 E[e^{-K_i t}] + E[e^{-2 K_i t}]$$

$$\text{and} \quad k_2 = V[e^{-K_i t}]$$

To develop equations giving the average growth increment and its variance for a particular population, we must know how  $L_i$  and  $K_i$  vary among the members of that population. There do not appear to be any data in the literature which could provide guidance on this point, so here it is assumed

that  $L_i$  is normally distributed (mean  $L_\infty$  and variance  $\sigma_{L_\infty}^2$ ) and  $K_i$  follows a gamma function with parameters  $r$  and  $\lambda$  (mean  $K = \frac{r}{\lambda}$  and variance  $\sigma_K^2 = \frac{r}{\lambda^2}$ ). These assumed distributions are probably realistic; one would expect  $\sigma_{L_\infty}^2$  to be small relative to  $L_\infty$  and so the normal distribution is probably adequate for  $L_i$ , whereas the gamma distribution allows considerable flexibility in the distribution of  $K_i$  while not permitting biologically meaningless (in this context) negative values. It can be shown (and I am indebted for this to Dr M.H. Smith) that if  $K_i$  follows a gamma distribution then

$$E[e^{-K_i t}] = \left(1 + \frac{\sigma_K^2 t}{K}\right)^{-\frac{K^2}{\sigma_K^2}}$$

Equations (i) and (ii) then become

$$E[I/l, t] = (L_\infty - 1) \left(1 - \left(1 + \frac{\sigma_K^2 t}{K}\right)^{-\frac{K^2}{\sigma_K^2}}\right) \quad \text{iii)}$$

$$\text{and} \quad V[I/l, t] = k_1 \sigma_{L_\infty}^2 + k_2 (L_\infty - 1)^2 \quad \text{iv)}$$

$$\text{where} \quad k_1 = 1 - 2 \left(1 + \frac{\sigma_K^2 t}{K}\right)^{-\frac{K^2}{\sigma_K^2}} + \left(1 + 2 \frac{\sigma_K^2 t}{K}\right)^{-\frac{K^2}{\sigma_K^2}}$$

$$\text{and} \quad k_2 = \left(1 + 2 \frac{\sigma_K^2 t}{K}\right)^{-\frac{K^2}{\sigma_K^2}} - \left(1 + \frac{\sigma_K^2 t}{K}\right)^{-\frac{2K^2}{\sigma_K^2}}$$

Equation (iii) gives the mean growth-increment for given initial length and time at liberty. A common method of estimating  $L_\infty$  and  $K$  from tag return data is to fit

$$E[I/l, t] = (L_\infty - 1) (1 - e^{-Kt}), \quad \text{v)}$$

usually where  $t$  is constant (i.e. the Ford-Walford plot and related methods - see Fabens, 1965). It is instructive to examine briefly the differences in behaviour of (iii) and (v). Values of  $\left[1 - (1 + \sigma_K^2 t/K)^{-K^2/\sigma_K^2}\right]$  are very similar to values of  $(1 - e^{-Kt})$  when  $\sigma_K^2$  is small relative to  $K$ , but as  $\sigma_K^2$  increases  $\left[1 - (1 + \sigma_K^2 t/K)^{-K^2/\sigma_K^2}\right]$  becomes progressively smaller than  $(1 - e^{-Kt})$ . Thus the effect of variability of  $K$  among members of a population is to decrease the average growth increment (at a given  $l$  and  $t$ ) relative to the prediction made assuming all animals had the same value of  $K$ . If  $\sigma_K^2 > 0$  and  $K$  is estimated by equation (v), the estimate obtained is negatively biased. If the estimate  $K'$  is obtained by fitting (v) when the values of  $L_i$  and  $K_i$  are distributed as described above, then

$$K' = \frac{K^2}{t\sigma_K^2} \ln \left( 1 + \frac{\sigma_K^2 t}{K} \right)$$

and the magnitude of the bias increases with increasing  $\sigma_K^2$  (relative to  $K$ ) and  $t$ . For example, if for a population  $K = 0.3$  and  $\sigma_K^2 = 0.01$  (time in years), then  $K'$  is 0.295 for growth increments measured over one year and 0.277 for increments measured over five years. In most cases the bias will be small (and probably negligible compared to other sources of bias, e.g. the effect of the tag on growth). Predictions of the average growth increment over some time interval using  $K'$  will not differ appreciably from those using  $K$ , provided the magnitude of the time interval is similar to the time at liberty of the tagged animals which were used to obtain  $K'$ .

It may be noted that a similar argument may be applied to use of the von Bertalanffy 'length at age' relationship, i.e. the length  $l_T$  of an animal at age  $T$  is

$$l_T = L_i \left( 1 - e^{-K_i T'} \right)$$

where

$$T' = T - T_0$$

This equation predicts the length at age  $t$  of an individual with growth parameters  $L_i$  and  $K_i$ . The mean length of a cohort at age  $T$  (assuming  $T_0$  is constant) is

$$E[l_T] = L_\infty \left( 1 - \left( 1 + \frac{\sigma_K^2 T'}{K} \right)^{-\frac{K^2}{\sigma_K^2}} \right) \quad (vi)$$

with variance  $V[l_T] = k_1 \sigma_{L_\infty}^2 + k_2 L_\infty^2$

where  $k_1$  and  $k_2$  are as for equation (iv) with  $t = T'$ .

## APPENDIX 3.3

A computer programme was written in Fortran IV to provide maximum likelihood estimates of the parameters of the growth equations (iii) and (iv) in Appendix 3.2.

Programme name: VBP (Von Bertalanffy Parameters)

Purpose: To find maximum likelihood estimations of the parameters  $L_{\infty}$ ,  $\sigma_{L_{\infty}}^2$ ,  $K$  and  $\sigma_K^2$  from tag return data, i.e. records of  $(I_i, l_i, t_i)$  where  $l_i$  is the initial length,  $t_i$  is the time at liberty and  $I_i$  is the growth increment ( $i = 1$  to  $n$ ). The population is assumed to consist of individuals, each of which possesses a specific pair of growth parameters  $(L_i, K_i)$ . The parameter values of each individual are assumed to be independent, with  $L_i$  normally distributed and  $K_i$  distributed as the gamma function among the members of the population. It is also assumed that the values of  $K_i$  and  $L_i$  possessed by an animal do not effect its probability of death (otherwise  $K$ ,  $L_{\infty}$ ,  $\sigma_K^2$  and  $\sigma_{L_{\infty}}^2$  must be treated as functions of length). An approximate confidence interval is calculated for each parameter.

Method: The equations to be fitted are

$$E[I/l, t] = (L_{\infty} - 1) \left[ 1 - \left( 1 + \frac{\sigma_K^2 t}{K} \right)^{-\frac{K^2}{\sigma_K^2}} \right]$$

$$V[I/l, t] = k_1 \sigma_{L_{\infty}}^2 + k_2 (L_{\infty} - 1)^2$$

where

$$k_1 = 1 - 2\left(1 + \frac{\sigma_K^2 t}{K}\right) - \frac{K^2}{\sigma_K^2} + \left(1 + \frac{2\sigma_K^2 t}{K}\right) - \frac{K^2}{\sigma_K^2}$$

and

$$k_2 = \left(1 + \frac{2\sigma_K^2 t}{K}\right) - \frac{K^2}{\sigma_K^2} - \left(1 + \frac{\sigma_K^2 t}{K}\right) - \frac{2K^2}{\sigma_K^2}$$

If  $L_i$  is normally distributed, then  $I_i$  has a symmetric distribution, and there is probably little error in considering  $I_i$  to be normally distributed. (Strictly, the probability density function of  $I$  should be obtained from the distributions of  $L_i$  and  $K_i$ .)

Thus, for  $n$  observations of  $(I_i, l_i, t_i)$ , the likelihood function is

$$L = \prod_{i=1}^{i=n} \frac{1}{\sigma_{I_i} \sqrt{2\pi}} e^{-\frac{(I_i - \hat{I}_i)^2}{2\sigma_{I_i}^2}}$$

$$\text{or } L = \ln L = -n \ln \sqrt{2\pi} - \frac{1}{2} \sum_{i=1}^{i=n} \ln \sigma_{I_i}^2 - \frac{1}{2} \sum_{i=1}^{i=n} \frac{(I_i - \hat{I}_i)^2}{\sigma_{I_i}^2}$$

where  $\hat{I}_i = E[I/l_i, t_i]$  and  $\sigma_{I_i}^2 = V[I/l_i, t_i]$  as provided above.

The Fletcher-Powell matrix modification method (Fletcher and Powell, 1963) is used to find the maximum value of  $L$ . This search is performed in subroutine FMFP, taken from Kuester and Mize (1973), which finds the minimum value of a function given its first derivatives. To obtain the maximum of  $L$  subroutine FMFP finds the minimum of  $-L$ .

The subroutine is constrained to yield non-negative parameter values by operating on the square roots of all parameters. Since the parameters may differ by several orders of magnitude they are further scaled such that the initial estimates of  $L_\infty$ ,  $K$ ,  $\sigma_K^2$  and  $\sigma_{L_\infty}^2$  to FMFP are 50, 4, 2 and 1 respectively. (The algorithm's performance is very sensitive to scaling. Inappropriate scaling is usually indicated if parameter 'movement' becomes very slow and the elements of the gradient vector differ by several orders of magnitude.)

Subroutine FCAL is also required and it calculates the function and derivative values at specified parameter values. The derivative of  $L$  with respect to parameter  $\theta_j$  ( $j = 1$  to 4) is

$$\frac{\partial L}{\partial \theta_j} = -\frac{1}{2} \sum_{i=1}^n \frac{\partial \sigma_{I_i}^2}{\partial \theta_j} \cdot \frac{1}{\sigma_{I_i}^2} + \sum_{i=1}^n \frac{(I_i - \hat{I}_i) \frac{\partial \hat{I}_i}{\partial \theta_j}}{\sigma_{I_i}^2} + \frac{1}{2} \sum_{i=1}^n \frac{(I_i - \hat{I}_i)^2 \frac{\partial \sigma_{I_i}^2}{\partial \theta_j}}{\sigma_{I_i}^4} \quad \text{i)}$$

and 
$$\frac{\partial -L}{\partial \theta_j} = - \frac{\partial L}{\partial \theta_j}$$

Subroutine FMFP operates on scaled parameter values,  $(X_j)$

$$\theta_j = S_j X_j^2$$

where  $S_j$  is a scale factor, and so

$$\frac{\partial -L}{\partial X_j} = - \frac{\partial L}{\partial \theta_j} \cdot 2 S_j X_j \quad \text{ii)}$$



The derivatives are calculated using equations (i) and (ii) and putting

$$\frac{\partial \hat{I}_i}{\partial L_\infty} = 1 - Z_i$$

$$\frac{\partial \sigma_{I_i}^2}{\partial L_\infty} = 2 (L_\infty - l_i) k_{2,i}$$

$$\frac{\partial \hat{I}_i}{\partial \sigma_{L_\infty}^2} = 0$$

$$\frac{\partial \sigma_{I_i}^2}{\partial \sigma_{L_\infty}^2} = k_{1,i}$$

$$\frac{\partial \hat{I}_i}{\partial K} = - (L_\infty - l_i) Z_i \psi_i$$

$$\frac{\partial \sigma_{I_i}^2}{\partial K} = \sigma_{L_\infty}^2 (\phi_i - 2Z_i \psi_i) + (L_\infty - l_i)^2 (\phi_i - 2Z_i^2 \psi_i)$$

$$\frac{\partial \hat{I}_i}{\partial \sigma_K^2} = - (L_\infty - l_i) Z_i \Delta_i$$

$$\frac{\partial \sigma_{I_i}^2}{\partial \sigma_K^2} = \sigma_{L_\infty}^2 (\omega_i - 2Z_i \Delta_i) + (L_\infty - l_i)^2 (\omega_i - 2Z_i^2 \Delta_i)$$

$$\text{where } k_{1,i} = 1 - 2 \left(1 + \frac{\sigma_K^2 t_i}{K}\right) \frac{-\frac{K^2}{\sigma_K^2}}{\sigma_K^2} + \left(1 + \frac{2\sigma_K^2 t_i}{K}\right) \frac{-\frac{K^2}{\sigma_K^2}}{\sigma_K^2}$$

$$k_{2,i} = \left(1 + \frac{2\sigma_K^2 t_i}{K}\right) \frac{-\frac{K^2}{\sigma_K^2}}{\sigma_K^2} - \left(1 + \frac{\sigma_K^2 t_i}{K}\right) \frac{-\frac{2K^2}{\sigma_K^2}}{\sigma_K^2}$$

$$\begin{aligned}
 z_i &= \left(1 + \frac{\sigma_K^2 t_i}{K}\right)^{-\frac{K^2}{\sigma_K^2}} \\
 \psi_i &= \frac{t_i}{1 + t_i \frac{\sigma_K^2}{K}} - \frac{2 K \ln\left(1 + \frac{t_i \sigma_K^2}{K}\right)}{\sigma_K^2} \\
 \phi_i &= \left(1 + \frac{2 t_i \sigma_K^2}{K}\right)^{-\frac{K^2}{\sigma_K^2}} \left[ \frac{2 t_i}{\left(1 + \frac{t_i \sigma_K^2}{K}\right)} - \frac{2 K \ln\left(1 + \frac{2 t_i \sigma_K^2}{K}\right)}{\sigma_K^2} \right] \\
 \omega_i &= \left(1 + \frac{2 t_i \sigma_K^2}{K}\right)^{-\frac{K^2}{\sigma_K^2}} \left[ -\frac{2 K t_i}{\sigma_K^2 \left(1 + \frac{2 t_i \sigma_K^2}{K}\right)} + \frac{K^2 \ln\left(1 + \frac{2 t_i \sigma_K^2}{K}\right)}{\sigma_K^4} \right] \\
 \Delta_i &= \frac{K t_i}{\sigma_K^2 \left(1 + \frac{t_i \sigma_K^2}{K}\right)} + \frac{K^2 \ln\left(1 + \frac{t_i \sigma_K^2}{K}\right)}{\sigma_K^4}
 \end{aligned}$$

Subroutine LIMIT calculates the confidence interval for each parameter in turn, considering that it is the only parameter which varies. Since

$$\sum_{i=1}^{i=n} \frac{(I_i - \hat{I}_i)^2}{\sigma_{I_i}^2}$$

is distributed as  $\chi^2$  with  $n$  degrees of freedom, a confidence region is obtained such that

$$\chi^2_{1-\frac{\alpha}{2}, n} \leq \sum_{i=1}^{i=n} \frac{(I_i - \hat{I}_i)^2}{\sigma_{I_i}^2} \leq \chi^2_{\frac{\alpha}{2}, n}$$

Beginning in each case with the maximum likelihood estimates of the parameters, each parameter is first increased and then decreased until a boundary is exceeded. A linear interpolation method is then repeatedly applied to obtain the boundary values of the parameter.

The confidence region established in this way is approximate. The  $\chi^2$  values are not independent of the values of the other three parameters, and it is possible that certain parameters are correlated. (The equations governing the confidence ellipsoid were not examined in any depth.)

Use: The data deck layout is as follows:

card	information	format
1	Heading	
2	Maximum number of iterations and the number of observations (ND)	2 I 10
3	estimate of minimum function value and the minimum sum of gradient vector which will terminate search (about $10^{-3}$ )	2 F 10.5
4	initial parameter estimates of $L_\infty$ , $K$ , $\sigma_K^2$ and $\sigma_{L_\infty}^2$ (in that order)	4 F 10.4
5 to ND+5	ND cards giving initial length, time at liberty and growth increment (in that order)	3 F 10.4
ND+6	$\chi^2_{\frac{\alpha}{2}, n}$ and $\chi^2_{(1 - \frac{\alpha}{2}), n}$	2 F 10.4
(This card is included only if confidence intervals are required.)		

In some cases it may be necessary to alter the parameter scale factors which are stored in array X

(in the order  $L_\infty$ ,  $K$ ,  $\sigma_K^2$  and  $\sigma_L^2$ ). Thus the initial value of  $\sigma_K^2$  passed to subroutine FMFP may be changed from 2 to 6 by replacing the statement

$$X(3) = 2,$$

in programme VBP by

$$X(3) = 6.$$

```

C 000:0000:5
C 000:0000:5
C 000:0000:5
START OF SEGMENT 002
WHAT SEGMENT IS OODC LONG
C 002:0000:0
C 002:0000:0
C 002:0000:0
C 002:0000:0
C 002:0000:0
C 002:0000:0
C 002:0000:0
C 002:0000:0
C 002:0001:0
C 002:0005:0
C FIB IS 0006 LONG
C 002:000C:2
C 002:000C:2
C FIB IS 0006 LONG
C 002:0013:2
C 002:0013:2
C 002:001D:2
C 002:001D:2
C 002:0026:2
C 002:0026:2
C 002:0026:2
C 002:0027:1
C 002:0034:2
C 002:0047:2
C 002:0047:2
C 002:0047:2
C 002:0047:2
C 002:0047:2
C 002:0048:4
C 002:0048:4
C 002:004A:0
C 002:004A:2
C 002:004C:0
C 002:004F:1
C 002:0051:2
C 002:0057:1
C 002:0057:1
C 002:0057:1
C 002:005B:2
C 002:005B:2
C 002:0066:2
C 002:0066:2
C 002:0066:2
C 002:006A:2
C 002:006A:2
C 002:0076:2
C 002:0076:2
C 002:0078:4
C 002:0078:4
C 002:0078:4
C 002:0078:4
C 002:0078:4
C 002:0079:5
C 002:007B:0
C 002:007C:2
C 002:007D:3
C 002:0080:2
C 002:0083:1
C 002:0086:2
C 002:0089:3
C 002:008B:1
C 002:008B:1
C 002:0092:2
C 002:0092:2
C 002:0093:0
C 002:0098:4
C 002:009C:2
C 002:009C:2
C 002:00A1:2
C 002:00A1:2
C 002:00A9:2
C 002:00A9:2
C 002:00B0:2
C 002:00B0:2
C 002:00B7:2
C 002:00B7:2
C 002:00BB:2
C 002:00BB:2
C 002:00C7:2
C 002:00C7:2
C 002:00C7:2
C 002:00C7:2

```

```

C
C
C      CALCULATE APPROXIMATE CONFIDENCE INTERVAL FOR PARAMETERS IF REQUIRED
C
      TEST=0.01*CHI2
      TEST2=0.01*CHI2L
      DO 100 I=1,4
100    AA(I)=X(I)
      CALL LIMIT(AA,VAL)
      CHIM=VAL
      WRITE(6,108)
108    FORMAT(/,5X,'CONFIDENCE INTERVAL FOR PARAMETERS',/,10X,'LOWER',21X
      *,'UPPER')
      S2=-1
      DO 101 I=1,4
      IF(I.GE.2)AA(I-1)=X(I-1)
      DO 102 K=1,2
      SS=S2**K
      AA(I)=X(I)
      ICOUNT=0
      LCOUNT=0
      STEP=0.1*AA(I)*SS
      IF(STEP.EQ.0.)STEP=0.001
C  FIND INITIAL VALUES OF CHI SQUARED
      VALL=CHIM
      AAL=AA(I)
      AA(I)=STEP+AA(I)
106    CALL LIMIT(AA,VAL)
      IF(VAL-CHI2)103,104,105
103    IF(VAL-CHI2L)125,104,123
C  IF CHI SQUARED LESS THAN CRITICAL DOUBLE STEP SIZE AND REPEAT
123    AAL=AA(I)
      VALL=VAL
      STEP=STEP+STEP
      AA(I)=AA(I)+STEP
      IF(AA(I).GT.0.)GO TO 110
C  PARAMETERS CONSIDERED BOUNDED 'NATURALLY' AT ZERO
      AA(I)=0.
      GO TO 104
110    LCOUNT=LCOUNT+1
      IF(LCOUNT.EQ.20)STEP=STEP*10
      IF(LCOUNT.EQ.40)STEP=STEP*10
      IF(LCOUNT.GE.50)STEP=STEP*10
      GO TO 106
105    CONTINUE
C  IF CHI SQUARED GREATER THAN CRITICAL LINEARLY INTERPOLATE
      ICOUNT=ICOUNT+1
      IF(ICOUNT.GT.30)GO TO 99
      GG=(VAL-VALL)/(AA(I)-AAL)
      AAR=AA(I)
      VALR=VAL
      AA(I)=(CHI2-VALL)/GG+AAL
      CALL LIMIT(AA,VAL)
      IF(ABS(VAL-CHI2).LE.TEST)GO TO 104
C  IF PARAMETER MOVEMENT LESS THAN 1 PERCENT TERMINATE SEARCH
      IF(VAL-CHI2)200,104,105
200    VALL=VAL
      VAL=VALR
      AAL=AA(I)
      AAR=AA(I)
      GO TO 105
125    CONTINUE
C  IF CHI SQUARED LESS THAN LOWER CRITICAL LINEARLY INTERPOLATE
      ICOUNT=ICOUNT+1
      IF(ICOUNT.GT.30)GO TO 99
      GG=(VAL-VALL)/(AA(I)-AAL)
      AAR=AA(I)
      VALR=VAL
      AA(I)=(CHI2L-VALL)/GG+AAL
      CALL LIMIT(AA,VAL)
      IF(ABS(VAL-CHI2L).LE.TEST2)GO TO 104
      IF(VAL-CHI2L)125,104,126
126    VALL=VAL
      AAL=AA(I)
      VAL=VALR
      AAR=AA(I)
      GO TO 125
99    WRITE(6,199)
199    FORMAT(5X,'LIMITS OF THE FOLLOWING PARAMETER NOT CONVERGED TO WITH
      IN ONE PERCENT IN 10 ITERATIONS')
104    BOUND(K)=AA(I)
      CHI(K)=VAL
102    CONTINUE
      WRITE(6,107)BOUND
107    FORMAT(10X,4(1PE16.8,10X))
101    CONTINUE
999    STOP
      END
002:015C14 IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEMENT AT 002:00C7

```

```

C 002:0001:0
C 002:0001:0
C 002:0001:0
C 002:0001:0
C 002:0004:0
C 002:0007:0
C 002:0008:0
C 002:000C:3
C 002:000E:2
C 002:000F:1
C 002:00E3:2
C 002:00E3:2
C 002:00E3:2
C 002:00E4:1
C 002:00E5:0
C 002:00E9:0
C 002:00EA:0
C 002:00EC:1
C 002:00EE:3
C 002:00EF:1
C 002:00EF:5
C 002:00F3:1
C 002:00F6:3
C 002:00F6:3
C 002:00F7:2
C 002:00F8:5
C 002:00FB:4
C 002:00F0:3
C 002:0100:5
C 002:0104:4
C 002:0104:4
C 002:0106:1
C 002:0107:0
C 002:0108:1
C 002:010A:2
C 002:010B:1
C 002:010B:1
C 002:010C:4
C 002:010D:1
C 002:010E:3
C 002:0110:5
C 002:0113:3
C 002:0116:1
C 002:0116:4
C 002:0116:4
C 002:0116:4
C 002:0118:0
C 002:0119:0
C 002:011C:0
C 002:011D:3
C 002:011E:2
C 002:0121:3
C 002:0123:2
C 002:0125:3
C 002:0125:3
C 002:0128:5
C 002:0129:4
C 002:012A:3
C 002:012C:0
C 002:012D:4
C 002:012E:1
C 002:012E:1
C 002:012E:1
C 002:012F:3
C 002:0130:3
C 002:0133:3
C 002:0135:0
C 002:0135:5
C 002:0139:0
C 002:013A:5
C 002:013D:0
C 002:0140:2
C 002:0141:1
C 002:0142:4
C 002:0143:3
C 002:0145:1
C 002:0145:4
C 002:0149:2
C 002:0149:2
C 002:0149:2
C 002:014D:2
C 002:014F:3
C 002:0156:2
C 002:0156:2
C 002:0158:3
C 002:0159:2

```

SEGMENT 002 IS 017E LONG

```

SUBROUTINE LIMIT(A,VAL)
DIMENSION A(4)
COMMON HD,SL(200),T(200),YI(200)
REAL LIML,LIML2,K1,K2
DO 1 I=1,HD
  TT=T(I)
  LIML=A(I)-SL(I)
  LIML2=LIML*LIML
  Z1=1.+(A(3)*TT)/A(2)
  Z2=1.+(A(3)*TT*2.)/A(2)
  Z3=Z2**(-A(2)*A(2)/A(3))
  Z=Z1**(-A(2)*A(2)/A(3))
  YH=LIML*(1.-Z)
  YH=YI(I)-YH
  YH2=YH*YH
  ZSQ=Z*Z
  K1=1.+Z3-2.*Z
  K2=Z3-ZSQ
  SIGI=K1*A(4)+K2*LIML2
  IF(SIGI.LE.0.)WRITE(6,505)(A(I),I=1,4),K1,K2
505  FORMAT(1X,'NEGATIVE VARIANCE] X VALUES',4E16.7,/,2X,'K1 AND K2',
      12X,2E16.7)
  PHI=YH2/SIGI+PHI
  VAL=PHI
  RETURN
END

```

```

START OF SEGMENT 006
C 006:0000:0
C 006:0000:0
C 006:0000:0
C 006:0000:0
C 006:0000:0
C 006:0001:0
C 006:0002:4
C 006:0004:4
C 006:0005:3
C 006:0009:1
C 006:0000:2
C 006:0012:3
C 006:0018:0
C 006:0019:4
C 006:001C:0
C 006:001C:5
C 006:001E:0
C 006:0020:1
C 006:0021:3
C 006:0024:4
C 006:0035:2
C 006:0035:2
C 006:0035:2
C 006:0039:3
C 006:003A:2
C 006:003A:5
SEGMENT 006 IS 0045 LONG

```

```

SUBROUTINE FMFP(FUNCT,H,M,X,F,G,EST,EPS,LIMIT,IER,H,KOUNT)
DIMENSION H(M),X(N),G(N)
C
C COMPUTE FUNCTION VALUE AND GRADIENT VECTOR FOR INITIAL ARGUMENT
101  WRITE(6,101)
      FORMAT(5X,'PARAMETER VALUES GIVEN FOR EACH ITERATION ARE SCALED',
1/5X,'ACTUAL VALUE=((SCALED VALUE)**2)*(INITIAL VALUE PROVIDED BY
 1USER)/(INITIAL SCALED VALUE)**2')
      CALL FUNCT(H,X,F,G)
C
C RESET ITERATION COUNTER AND GENERATE IDENTITY MATRIX
C
  IER=0
  KOUNT=0
  N2=N+N
  N3=N2+N
  N31=N3+1
  1  K=N31
      DO 4 J=1,N
        H(K)=1.
        NJ=N-J
        IF(NJ) 5,5,2
      2  DO 3 L=1,NJ
        KL=K+L
      3  H(KL)=0.
      4  K=KL+1
C
C START ITERATION LOOP
C
  5  KOUNT=KOUNT+1
      WRITE(6,501)
501  FORMAT(//)
      WRITE(6,100)KOUNT,X,F
100  FORMAT(1X,'BEGINNING ITERATION '13,'PARAMETER VALUES',4(2X,F7.3),1
      1X,'FUNCTION='1,F6.2)
C THE C IN COLUMN ONE OF THE FOLLOWING CARD
C TO OUTPUT GRADIENT VECTOR AT BEGINNING OF EACH ITERATION REMOVE
C WRITE(6,500)G
500  FORMAT(5X,'GRADIENT VECTOR',2X,4(E16.8,10X))
C
C SAVE FUNCTION VALUE, ARGUMENT VECTOR AND GRADIENT VECTOR
104  OLDF=F
      DO 9 J=1,N
        K=N+J
        H(K)=G(J)
        K=K+N
        H(K)=X(J)
C
C DETERMINE DIRECTION VECTOR H.
C
      K=J+N3
      T=0.
      DO 8 L=1,N
        T=G(L)*H(K)
      IF(L-J) 6,7,7
      6  K=K+N-L
      GO TO 8
      7  K=K+1
      8  CONTINUE
      9  H(J)=T
C
C CHECK WHETHER FUNCTION WILL DECREASE STEPPING ALONG H.

```

```

START OF SEGMENT 007
C 007:0000:0
C 007:0000:0
C 007:0000:0
C 007:0000:0
C 007:0000:0
C 007:0004:2
C 007:0004:2
C 007:0004:2
C 007:0004:2
C 007:0004:2
C 007:0008:5
C 007:0008:5
C 007:0008:5
C 007:0009:3
C 007:000A:1
C 007:000B:3
C 007:000C:4
C 007:000D:4
C 007:000E:3
C 007:0010:0
C 007:0012:0
C 007:0013:3
C 007:0014:2
C 007:0015:0
C 007:0016:3
C 007:001A:4
C 007:001E:1
C 007:001E:1
C 007:001E:1
C 007:001F:3
C 007:0023:2
C 007:0023:2
C 007:002F:2
C 007:002F:2
C 007:002F:2
C 007:002F:2
C 007:002F:2
C 007:002F:2
C 007:002F:2
C 007:0030:1
C 007:0031:0
C 007:0032:3
C 007:0035:3
C 007:0037:0
C 007:003A:0
C 007:003A:0
C 007:003A:0
C 007:003B:3
C 007:003C:1
C 007:003D:0
C 007:0041:1
C 007:0042:3
C 007:0044:3
C 007:0045:0
C 007:0046:2
C 007:0048:3
C 007:004C:5
C 007:004C:5
SEGMENT 008 IS 000A LONG

```

```

C      DY=0.
C      HNRH=0.
C      GNRH=0.
C
C      CALCULATE DIRECTIONAL DERIVATIVE AND TEST VALUES FOR DIRECTION
C      VECTOR H AND GRADIENT VECTOR G.
C      DO 10 J=1,N
C      HNRH=HNRH+ABS(H(J))
C      GNRH=GNRH+ABS(G(J))
10  DY=DY+H(J)*G(J)
C
C      REPEAT SEARCH IN DIRECTION OF STEEPEST DESCENT IF DIRECTIONAL
C      DERIVATIVE APPEARS TO BE POSITIVE OR ZERO.
C      IF(DY) 11,51,51
C
C      REPEAT SEARCH IN DIRECTION OF STEEPEST DESCENT IF DIRECTION
C      VECTOR H IS SMALL COMPARED TO GRADIENT VECTOR G.
11  IF(HNRH/GNRH-EPS) 51,51,12
C
C      SEARCH MINIMUM ALONG DIRECTION H
C
C      SEARCH ALONG H FOR POSITIVE DIRECTIONAL DERIVATIVE
12  FY=F
C      ALFA=2.*(EST-F)/DY
C      AMBDA=1.
C
C      USE ESTIMATE FOR STEPSIZE ONLY IF IT IS POSITIVE AND LESS THAN
C      1. OTHERWISE TAKE 1. AS STEPSIZE
C      IF(ALFA) 15,15,13
13  IF(ALFA-AMBDA) 14,15,15
14  AMBDA=ALFA
15  ALFA=0.
C
C      SAVE FUNCTION AND DERIVATIVE VALUES FOR OLD ARGUMENT
16  FX=FY
C      DX=DY
C
C      STEP ARGUMENT ALONG H
C      DO 17 I=1,N
17  X(I)=X(I)+AMBDA*H(I)
C
C      COMPUTE FUNCTION VALUE AND GRADIENT FOR NEW ARGUMENT
C      CALL FUNCT(N,X,F,G)
C
C      FY=F
C
C      COMPUTE DIRECTIONAL DERIVATIVE DY FOR NEW ARGUMENT, TERMINATE
C      SEARCH, IF DY IS POSITIVE, IF DY IS ZERO THE MINIMUM IS FOUND
C      DY=0.
C      DO 18 I=1,N
18  DY=DY+G(I)*H(I)
C      IF(DY) 19,36,22
C
C      TERMINATE SEARCH ALSO IF THE FUNCTION VALUE INDICATES THAT
C      A MINIMUM HAS BEEN PASSED
19  IF(FY-FX) 20,22,22
C
C      REPEAT SEARCH AND DOUBLE STEPSIZE FOR FURTHER SEARCHES
20  AMBDA=AMBDA+ALFA
C      ALFA=AMBDA
C
C      END OF SEARCH LOOP
C
C      TERMINATE IF THE CHANGE IN ARGUMENT GETS VERY LARGE
C      IF(HNRH*AMBDA-1.E10) 16,16,21
C
C      LINEAR SEARCH TECHNIQUE INDICATES THAT NO MINIMUM EXISTS
21  IER=2
C      RETURN
C
C      INTERPOLATE CUBICALLY IN THE INTERVAL DEFINED BY THE SEARCH
C      ABOVE AND COMPUTE THE ARGUMENT X FOR WHICH THE INTERPOLATION
C      POLYNOMIAL IS MINIMIZED
22  T=0.
23  IF(AMBDA) 24,36,24
24  Z=3.*(FX-FY)/AMBDA+DX+DY
C      ALFA=AMAX1(ABS(Z),ABS(DX),ABS(DY))
C      DALFA=Z/ALFA
C      DALFA=DALFA*DALFA-DX/ALFA*DY/ALFA
C      IF(DALFA) 51,25,25
25  W=ALFA*SQRT(DALFA)
C      ALFA=(DY+W-Z)*AMBDA/(DY+2.*W-DX)
C      DO 26 I=1,N
26  X(I)=X(I)+(T-ALFA)*H(I)
C
C      TERMINATE, IF THE VALUE OF THE ACTUAL FUNCTION AT X IS LESS
C      THAN THE FUNCTION VALUES AT THE INTERVAL ENDS. OTHERWISE REDUCE
C      THE INTERVAL BY CHOOSING ONE END-POINT EQUAL TO X AND REPEAT
C      THE INTERPOLATION. WHICH END-POINT IS CHOSEN DEPENDS ON THE
C      VALUE OF THE FUNCTION AND ITS GRADIENT AT X.
C
C      CALL FUNCT(N,X,F,G)
C
C      IF(F-FX) 27,27,28
C      IF(F-FY) 36,36,28
28  DALFA=0.
C      DO 29 I=1,N
29  DALFA=DALFA+G(I)*H(I)
C      IF(DALFA) 30,33,33
30  IF(F-FX) 32,31,33
31  IF(DX-DALFA) 32,36,32

```

```

C 007:004C:5
C 007:004D:3
C 007:004E:1
C 007:004E:5
C 007:004E:5
C 007:004E:5
C 007:0050:0
C 007:0052:5
C 007:0055:4
C 007:005C:0
C 007:005C:0
C 007:005C:0
C 007:005D:4
C 007:005D:4
C 007:005D:4
C 007:005D:4
C 007:0060:0
C 007:0060:0
C 007:0060:0
C 007:0060:0
C 007:0060:5
C 007:0063:1
C 007:0063:5
C 007:0063:5
C 007:0063:5
C 007:0065:0
C 007:0066:2
C 007:0067:1
C 007:0067:5
C 007:0067:5
C 007:0067:5
C 007:0068:4
C 007:0069:3
C 007:0069:3
C 007:0069:3
C 007:0068:0
C 007:0071:3
C 007:0071:3
C 007:0071:3
SEGMENT 009 IS 000A LONG
C 007:0076:0
C 007:0076:5
C 007:0076:5
C 007:0076:5
C 007:0076:5
C 007:0077:3
C 007:0079:0
C 007:007F:2
C 007:0082:1
C 007:0082:1
C 007:0082:1
C 007:0082:1
C 007:0084:0
C 007:0084:0
C 007:0084:0
C 007:0085:2
C 007:0085:5
C 007:0085:5
C 007:0085:5
C 007:0089:1
C 007:0089:1
C 007:0089:1
C 007:008A:0
C 007:008A:3
C 007:008A:3
C 007:008A:3
C 007:008B:1
C 007:008C:2
C 007:008F:4
C 007:0095:1
C 007:0096:3
C 007:0099:2
C 007:009A:1
C 007:009C:1
C 007:00A0:3
C 007:00A2:0
C 007:00A9:0
C 007:00A9:0
C 007:00A9:0
C 007:00A9:0
C 007:00A9:0
C 007:00A9:0
C 007:00A9:0
SEGMENT 00B IS 000A LONG
C 007:00AD:3
C 007:00AE:5
C 007:00B0:1
C 007:00B0:5
C 007:00B2:0
C 007:00B8:2
C 007:00B9:3

```





		START OF SEGMENT 00D
C	SUBROUTINE FUNCT(N,ARG,VAL,GRAD)	C 00D:0000:0
C	ARGUMENT LIST	C 00D:0000:0
C	ARG = VECTOR OF X VALUES.	C 00D:0000:0
C	VAL = OBJECTIVE FUNCTION EQUATION.	C 00D:0000:0
C	GRAD = VECTOR OF OBJECTIVE FUNCTION DERIVATIVES, (N LONG).	C 00D:0000:0
C	DIMENSION ARG(N), GRAD(N)	C 00D:0000:0
C	COMMON ND, SL(200), T(200), YI(200), S(7)	C 00D:0000:0
C	DIMENSION A(4)	C 00D:0000:0
C	DOUBLE PRECISION LIML, LIML2, Z, Z1, Z2, Z3, PH, TH, DT, YH, YH2, K1, K2, ZSQ	C 00D:0000:0
C	*, SIGI, SIGI2, TPS, TPY, F(4), OM	C 00D:0000:0
C	MODEL: $E[(1/SL, T)] = (L - SL) \{ 1 - (1 + (V[K]*T)/E[K])^{*} (-E[K]^{*}2/V[K]) \}$	C 00D:0000:0
C	$V[1/SL, T] = K(SUB 1)*V[L] + K(SUB 2)*(L - SL)*(L - SL)$	C 00D:0000:0
C	WHERE L AND K ARE PARAMETERS OF AN INDIVIDUAL ANIMALS GROWTH;	C 00D:0000:0
C	SL=INITIAL LENGTH; I=GROWTH INCRIMENT; T=TIME AT LIBERTY	C 00D:0000:0
C	NN=ND	C 00D:0000:0
C	DO 3 I=1,4	C 00D:0000:0
C	F(I)=0.	C 00D:0001:0
3	A(I)=S(I)*ARG(I)*ARG(I)	C 00D:0002:0
C	VAL=0.	C 00D:0003:4
C	FOR OUTPUT ON EACH ITERATIONS SEARCH, REMOVE C FROM FOLLOWING CARD	C 00D:0008:5
C	WRITE(6,10)A	C 00D:000C:3
10	FORMAT(5X, 'X VALUES ', 4(2X, E16.8))	C 00D:000C:3
C	VH=1.	C 00D:000C:3
C	CALCULATE ELEMENTS USED TO OBTAIN PARTIAL DERIVATIVES	C 00D:000D:1
C	DO 1 I=1,ND	C 00D:000D:1
C	LIML=A(I)-SL(I)	C 00D:000E:0
C	LIML2=LIML*LIML	C 00D:0010:0
C	TT=T(I)	C 00D:0010:5
C	Z1=1.+(A(3)*TT)/A(2)	C 00D:0012:3
C	Z2=1.+(A(3)*TT*2.)/A(2)	C 00D:0015:2
C	Z3=Z2*(-A(2)*A(2)/A(3))	C 00D:0018:4
C	Z=Z1*(-A(2)*A(2)/A(3))	C 00D:001C:3
C	PH=2.*Z3*((TT/Z2)-(A(2)*DLOG(Z2))/A(3))	C 00D:0020:4
C	TH=TT/Z1-2.*A(2)*DLOG(Z1)/A(3)	C 00D:0025:4
C	OM=Z3*(-2.*A(2)*TT/(A(3)*Z2)+A(2)*A(2)*DLOG(Z2)/(A(3)*A(3)))	C 00D:002A:1
C	DT=-A(2)*TT/(A(3)*Z1)+A(2)*A(2)*DLOG(Z1)/(A(3)*A(3))	C 00D:0032:2
C	YH=LIML*(1.-Z)	C 00D:0039:3
C	YH=YI(I)-YH	C 00D:003B:1
C	YH2=YH*YH	C 00D:003D:3
C	ZSQ=Z*Z	C 00D:003E:2
C	K1=1.+Z3-2.*Z	C 00D:003F:3
C	K2=Z3-ZSQ	C 00D:0041:4
C	SIGI=K1*A(4)+K2*LIML2	C 00D:0043:0
C	SIGI2=SIGI*SIGI	C 00D:0045:4
C	ACCUMULATE GRADIENT VECTOR	C 00D:0046:3
C	TPY=1.-Z	C 00D:0046:3
C	TPS=2.*K2*LIML	C 00D:0047:4
C	F(1)=0.5*TPS/SIGI-YH*TPY/SIGI -0.5*YH2*TPS/SIGI2+F(1)	C 00D:0049:3
C	TPY=-LIML*Z*TH	C 00D:0052:2
C	TPS=A(4)*(PH-2.*Z*TH)+LIML2*(PH-2.*Z*Z*TH)	C 00D:0054:2
C	F(2)=0.5*TPS/SIGI-YH*TPY/SIGI -0.5*YH2*TPS/SIGI2+F(2)	C 00D:005A:3
C	TPY=-LIML*Z*DT	C 00D:0063:2
C	TPS=A(4)*(OM-2.*Z*DT)+LIML2*(OM-2.*Z*Z*DT)	C 00D:0065:2
C	F(3)=0.5*TPS/SIGI-YH*TPY/SIGI -0.5*YH2*TPS/SIGI2+F(3)	C 00D:006B:3
C	TPY=0.	C 00D:0074:2
C	TPS=K1	C 00D:0075:1
C	F(4)=0.5*TPS/SIGI-YH*TPY/SIGI -0.5*YH2*TPS/SIGI2+F(4)	C 00D:0076:0
C	ACCUMULATE FUNCTION VALUE	C 00D:007E:2
C	VAL=0.5*(DLOG(SIGI)+YH2/SIGI)+VAL	C 00D:0083:2
1	CONTINUE	C 00D:0085:4
C	SCALE GRADIENT VECTOR	C 00D:0085:4
C	DO 2 I=1,4	C 00D:0085:4
2	GRAD(I)=F(I)*2.*S(I)*ARG(I)	C 00D:0087:0
C	ADD ND*LOG(SQRT(2*PI)) TO VAL	C 00D:008F:5
C	VAL=VAL+0.9189385*NN	C 00D:008F:5
C	FOR OUTPUT ON EACH ITERATIONS SEARCH, REMOVE C FROM FOLLOWING CARD	C 00D:0093:1
C	WRITE(6,11) GRAD, VAL	C 00D:0093:1
11	FORMAT(5X, 'GRAD ', 4(2X, E16.8), 5X, 'VAL= ', E16.8)	C 00D:0093:1
C	RETURN	C 00D:0093:4
C	END	C 00D:0093:4

SEGMENT 00D IS 00A2 LONG

FORMAT SEGMENT IS 0069 LONG  
 START OF SEGMENT 010  
 SEGMENT 011 IS 000A LONG  
 SEGMENT 010 IS 004A LONG

NO ERRORS DETECTED. NUMBER OF CARDS = 520.  
 COMPILATION TIME = 71 SECONDS ELAPSED. 6.39 SECONDS PROCESSING.  
 D2 STACK SIZE = 23 WORDS. FILESIZE = 140 WORDS. ESTIMATED CORE STORAGE REQUIREMENT = 2016 WORDS.  
 TOTAL PROGRAM CODE = 1125 WORDS. ARRAY STORAGE = 672 WORDS.  
 NUMBER OF PROGRAM SEGMENTS = 19. NUMBER OF DISK SEGMENTS = 91.  
 PROGRAM CODE FILE = (Z00LO33)A ON PACK, COMPILER COMPILED ON 01/31/77(FORTRAN ON PACK)

PERAKI TAG RETURN, T>0.5 YEARS  
FLETCHER POWELL ALGORITHM

PARAMETERS

N = 4    LIMIT = 90    EST = .20000000E+01    EPS = .10000000E-02

INITIAL VALUES

L INFINITY= 1.30000000E+01  
K= 1.50000000E-01  
VARIANCE OF K= 1.00000000E-02  
VARIANCE OF L INFINITY= 1.00000000E+00  
PARAMETER VALUES GIVEN FOR EACH ITERATION ARE SCALED.  
ACTUAL VALUE=((SCALED VALUE)\*\*2)\*((INITIAL VALUE PROVIDED BY USER)/(INITIAL SCALED VALUE)\*\*2)

BEGINNING ITERATION	1PARAMETER VALUES	50.000	4.000	2.000	1.000	FUNCTION= 6.85
BEGINNING ITERATION	2PARAMETER VALUES	50.139	4.209	2.153	1.265	FUNCTION= 4.11
BEGINNING ITERATION	3PARAMETER VALUES	50.196	4.297	2.112	1.200	FUNCTION= 4.08
BEGINNING ITERATION	4PARAMETER VALUES	50.348	4.227	2.125	1.170	FUNCTION= 4.07
BEGINNING ITERATION	5PARAMETER VALUES	50.348	4.227	2.125	1.170	FUNCTION= 4.07
BEGINNING ITERATION	6PARAMETER VALUES	50.341	4.201	2.148	1.203	FUNCTION= 4.05
BEGINNING ITERATION	7PARAMETER VALUES	50.338	4.193	2.147	1.200	FUNCTION= 4.05
BEGINNING ITERATION	8PARAMETER VALUES	50.377	4.180	2.163	1.183	FUNCTION= 4.05
BEGINNING ITERATION	9PARAMETER VALUES	50.382	4.177	2.170	1.180	FUNCTION= 4.05
BEGINNING ITERATION	10PARAMETER VALUES	50.381	4.178	2.173	1.178	FUNCTION= 4.05

MINIMIZATION PROCEDURE COMPLETED

IER = 0    NUMBER OF ITERATIONS = 10

MINIMUM VALUE OF F = 4.05185217E+00

FINAL GRADIENT VECTOR  
.30541581E-05    -.33332962E-05    -.73995104E-05    -.14244898E-04

FINAL VALUES

L INFINITY= 1.31906323E+01  
K= 1.63617970E-01  
VARIANCE OF K= 1.18062349E-02  
VARIANCE OF L INFINITY= 1.38741756E+00

CONFIDENCE INTERVAL FOR PARAMETERS

LOWER	UPPER
1.25869566E+01	1.64461811E+01
1.10399764E-01	3.37671316E-01
6.43287011E-03	2.43627410E-02
6.36656745E-01	2.94884002E+00

## APPENDIX 7.1

The population model described in Chapter 1 involves a considerable amount of data manipulation and computation, so non-trivial applications of the model require the use of a computer. The following computer programme, written in FORTRAN IV, utilizes the population model to calculate the yield per recruitment under various patterns of size specific fishing mortality. In that these calculations involve the construction of a projection matrix, multiplication of a population vector by the projection matrix and calculation of the yield of the fishery during the time period simulated by one such multiplication, the yield per recruitment analysis demonstrates most of the main programme segments required for application of the population model. The programme does not illustrate the use of reproduction terms in the matrix, nor does it involve finding the eigenvalues and eigenvectors of the projection matrix. Reproductive terms may easily be incorporated into the projection matrix directly (as given in Chapter 1) or the total recruitment may be calculated separately for each time interval and added to the population vector. The projection matrix may be solved for its eigenvalues and eigenvectors by utilizing one of a number of suitable sub-programmes available at most computer installations, e.g. the Burroughs NUMERALS package programme MATHLIB/SYMBOL/NONSYPEIGENVALUES which utilizes the algorithm given in Martin, Peters and Wilkinson (1970).

The programme presented here was not written to be highly efficient in terms of storage requirements and execution time (although these were, of course, borne in mind); one of the main functions of the programme is to illustrate the construction and use of the size class population model.

Programme name: SCYPR (Size, Class, Yield, per Recruitment)

Method: The main features of the main-line programme are provided by the flow chart in Fig. I.

The main-line programme calls three subroutines (PROB, ZLOAD and GEN) which construct and use the population projection matrix. The mean (GBAR) and standard deviation (SG) of length at time  $T+1$  of animals initially in size class  $j$  are calculated from the growth function in the main-line programme and passed to subroutine PROB via the CALL statement. Each call to this subroutine relates to one source size class ( $j$ ,  $j = 1$  to  $N$ ). Subroutine PROB calculates the  $P_{i,j}$  terms of the projection matrix (the proportion of animals in class  $j$  at time  $T$  which will grow to be in class  $i$  at time  $T+1$ ). Representing length by  $L$ , each  $P_{i,j}$  = probability that  $(L \leq L_{ui})$  - probability that  $(L \leq L_{li})$ , where  $L_{ui}$  is the upper limit of size class  $i$  and  $L_{li}$  is the lower limit of size class  $i$ . The probabilities are calculated in subroutine PROBN which incorporates the chosen distribution of lengths at  $T+1$  (in this case the normal distribution). At the end of subroutine PROB a check is made that  $\sum_{i=1}^{i=N} P_{i,j} = 1.0$  for each  $j$ , i.e. all 'animals' grow to some final length within the size range

determined by the population vector. This condition is not satisfied if the growth function requires more size classes than are provided by the user, which would result in some animals 'growing out' of the population vector. The problem also arises when the growth increment is assumed to be normally distributed (as here) because this distribution has an infinite domain. In this case the discrepancy  $(1 - \sum_{i=1}^{i=N} P_{i,j})$  is very small and there is little error in adding it to the proportion growing into the largest size class,  $P_{n,j}$ , i.e. the infinite tail is compressed into the largest size class. This does, however, highlight the inadequacy of assuming the growth increment to be normally distributed, and it is hoped that this limitation (caused by incomplete knowledge of the growth process) will be overcome in future work.

Subroutine ZLOAD constructs the projection matrix from size specific mortality rates (natural and fishing) and the matrix of  $P_{i,j}$  values generated by subroutine PROB. The projection matrix is constructed in accordance with the equations given in Chapter 1.

Subroutine GEN calculates the population vector at some  $T+1$  given the population vector at time  $T$  and a size class projection matrix without fecundity terms or the possibility of negative growth. (Both of these conditions are eliminated most simply by changing the statement 'DO 15 K = I,NN' to 'DO 15 K = 1,NN'.) The size specific yield in numbers obtained during the period  $T$  to  $T+1$ , is also calculated in subroutine GEN, and is passed back to the main line programme in array YIELD. The yield equations

Data card	Information	Format
1	size class width (SW) number of size classes (N) maximum iteration (MAXITS)	F10.5,2I3
2	recruitment vector in size classes of specified width (may be more than one card)	8F10.5
3	growth parameters $(L_{\infty}, \sigma_{L_{\infty}}^2, K, \sigma_K^2)$	4F10.5
4	size specific natural mortality for size classes of specified width (may be more than one card)	8F10.5
5	heading	13A6,A2
6	size specific fishing mortality for size classes of specified width (may be more than one card)	8F10.5
7	NEXT in first 4 columns	A6
8	As for cards 4 - 7	

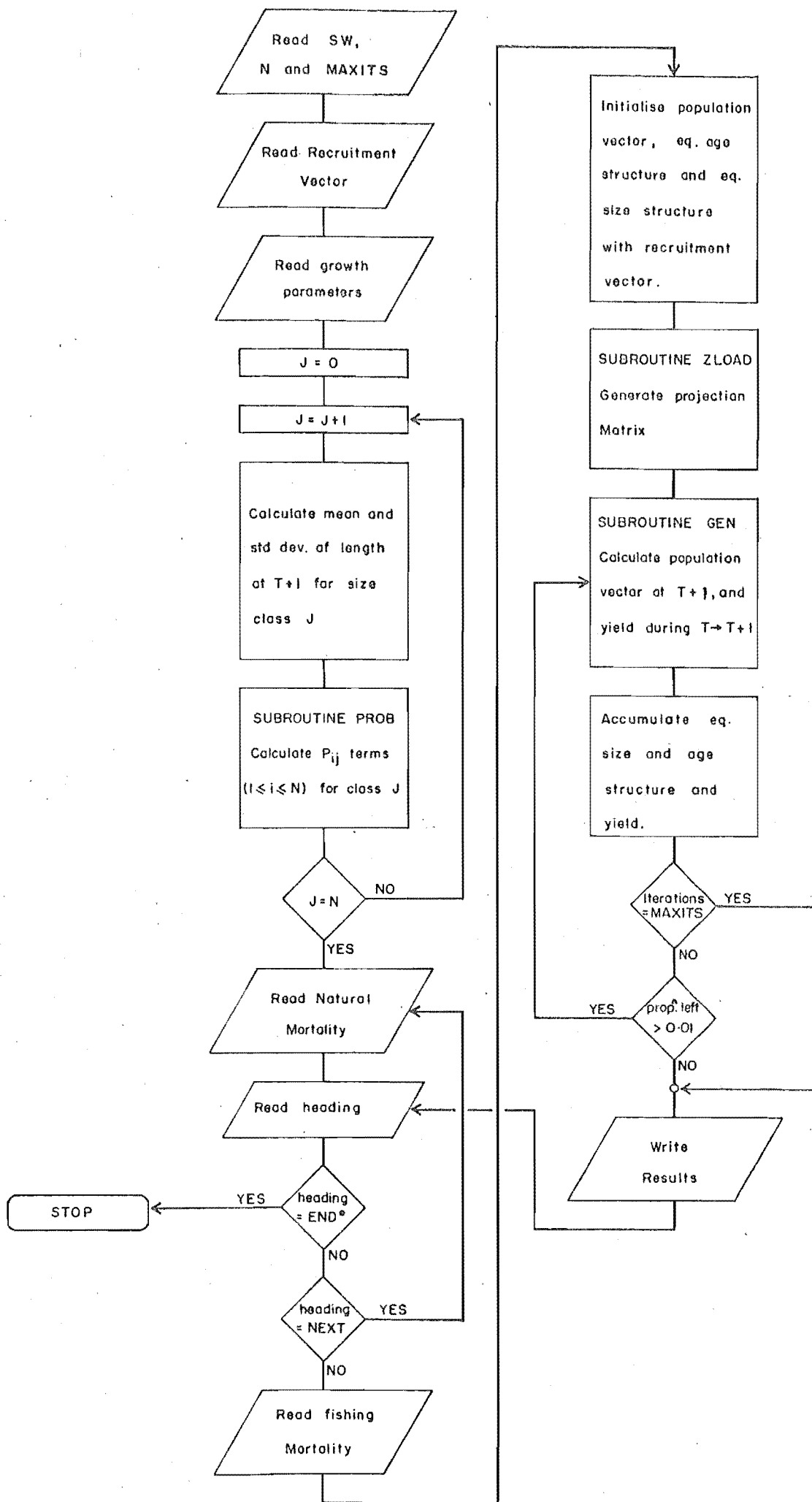
} repeatable

Fig. I Flow chart of main-line programme for SCYPR.

The following variable names are used:

N = number of size classes; SW = size class width;  
MAXITS = maximum number of years any recruitment  
is followed. END\* = the 'end of data' condition  
for the input file.





```

C      PROGRAM SCYPR,CALCULATES YIELDS PER RECRUIT USING SIZE CLASS
C      POPULATION MODEL.
C
C      DIMENSION REC(200)
C      DIMENSION YIELD(200),POPVEC(200),AS(200),SS(200),TOTY(200),HEAD(14
*)
C      COMMON/MORT/MORTP(200),MORTQ(200)
C      REAL L,MORTP,MORTQ
C      DATA CRD/'NEXT '/
C
C      READ SIZE CLASS WIDTH(SW),NUMBER OF SIZE CLASSES(N),AND MAXIMUM
C      NUMBER OF TIMES THROUGH INNER LOOP(MAXITS)
C      READ(5,1)SW,N,MAXITS
C
1      FORMAT(F10.5,2I3)
C      READ VECTOR OF SIZE SPECIFIC RECRUITMENT
C      READ(5,2)(REC(I),I=1,N)
2      FORMAT(8F10.5)
C      DO 23 I=1,N
23      RECT=REC(I)+RECT
C      CO=0.01*RECT
C      TT=1.
C      SW2=SW/2.
C      READ VALUES OF GROWTH PARAMETERS.VBL=L INFINITY,VLI=VARIANCE OF
C      L INFINITY,VBK=K,VK=VARIANCE OF K.CV=VARIANCE OF LENGTH FOR SIZE
C      CLASS WIDTH SW
C      ENSURE THAT UNITS OF PARAMETERS ARE THE SAME AS THOSE USED FOR SW
C      READ(5,2)VBL,VLI,VBK,VK
C      WRITE(6,40)RECT,VBL,VLI,VBK,VK
C
40      FORMAT(5X,'YIELD PER RECRUITMENT ANALYSIS USING SIZE CLASS POPULAT
*)
C      *ION MODEL,ALL CALCULATIONS BASED ON',F9.1,' RECRUITS',/,5X,'WITH
C      *THE FOLLOWING GROWTH PARAMETERS',/,15X,'L INFINITY=',F10.5,/,3X,'V
C      *ARIANCE OF L INFINITY=',F10.5,/,24X,'K=',F10.5,/,12X,'VARIANCE OF
C      *K=',F10.5)
C      CV=SW*SW/12.
C      TK=(1.+TT*VK/VBK)**(-VBK*VBK/VK)
C      TJ=(1.+2.*TT*VK/VBK)**(-VBK*VBK/VK)
C      TEMP=1.-TK
C      CALCULATE MEAN AND VARIANCE OF LENGTH AT T+1 FOR EACH SIZE CLASS,
C      THEN CALCULATE P(I,J) TERMS IN SUBROUTINE PROB
C      DO 4 I=1,N
C      L=(I-1)*SW+SW2
C      GBAR=(VBL*TEMP)-(TEMP*L)
C      IF(GBAR.LT.0.)GBAR=0.
C      GBAR=GBAR+L
C      IF(L.GE.6.)GO TO 100
C      Q=L*10.
C      T2=(-22.2506+SQRT(503.6236-4.9412*Q))/(-2.4706)
C      T2=T2+1.
C      GBAR=1.7272+22.2506*T2-1.2353*T2*T2
C      GBAR=GBAR/10.
100      CONTINUE
C      TK1=1.-2.*TK+TJ
C      TK2=TJ-TK*TK
C      VI=TK1*VLI+TK2*(VBL-L)*(VBL-L)
C      IF(VBL.LT.L) VI=TK1*VLI
C      IF(VI.LT.0.)WRITE(6,41)I
41      FORMAT(/,10X,'WARNING:NEGATIVE VARIANCE OF GROWTH INCREMENT OBTAIN
*)
C      *ED FOR SIZE CLASS',I5)
C      V=VI+CV*TK*TK+CV*TK2
C      VG=SQRT(V)
C      CALL PROB(I,GBAR,VG,IX,N,SW)
4      IF(IX.EQ.1)GO TO 999
C      READ VECTOR OF SIZE SPECIFIC NATURAL INSTANTANEOUS MORTALITY
111      READ(5,2,END=999)(MORTQ(I),I=1,N)
C      READ(5,5,END=999)HEAD
6      IF(HEAD(1).EQ.CRD)GO TO 111
C      WRITE(6,101)HEAD
5      FORMAT(13A6,A2)
101      FORMAT(////,5X,13A6,A2,////)
C      READ VECTOR OF SIZE SPECIFIC INSTANTANEOUS FISHING MORTALITY
C      READ(5,2)(MORTP(I),I=1,N)
C      LOAD POPULATION VECTOR WITH INITIAL RECRUITMENT
C      DO 24 I=1,N
C      RI=REC(I)
24      POPVEC(I)=RI
C      SS(I)=RI
C      AS(I)=RECT
C      GENERATE SIZE CLASS PROJECTION MATRIX IN SUBROUTINE ZLOAD
C      CALL ZLOAD(N)
C      ITERATIVELY FOLLOW FATE OF RECRUITMENT FOR A MAXIMUM OF 'MAXITS'
C      YEARS OR UNTIL LESS THAN ONE PERCENT REMAIN
C      DO 10 I=1,MAXITS
C      DEN=0.
C      SIZE STRUCTURE AFTER ONE YEAR,AND YIELD DURING THAT YEAR,
C      CALCULATED IN SUBROUTINE GEN
C      CALL GEN(POPVEC,YIELD,DEN,N)
C      EQUILIBRIUM AGE STRUCTURE ACCUMULATED IN ARRAY AS
C      AS(I+1)=DEN
C      EQUILIBRIUM SIZE STRUCTURE ACCUMULATED IN ARRAY SS
C      SIZE SPECIFIC YIELD ACCUMULATED IN ARRAY TOTY

```

	DO 11 J=1,N	C 002:00C0:0
	SS(J)=POPVEC(J)+SS(J)	C 002:00C1:0
	TOTY(J)=YIELD(J)+TOTY(J)	C 002:00C3:5
11	YIELD(J)=0.	C 002:00C6:4
C	TERMINATE IF LESS THAN 1% OF RECRUITS LEFT	C 002:00CA:2
	IF(DEN.LT.CO)GO TO 12	C 002:00CA:2
10	CONTINUE	C 002:00CB:4
	WRITE(6,13)DEN	C 002:00CD:5
13	FORMAT(5X,'MORE THAN 10 PERCENT OF INITIAL POPULATION LEFT AFTER	C 002:00D4:2
	*MAXIMUM ITERATIONS',/,5X,' NUMBER LEFT= ',F10.2)	C 002:00D4:2
12	WRITE(6,14)	C 002:00D4:2
14	FORMAT(5X,'EQUILIBRIUM AGE STRUCTURE(IN YEAR CLASSES)')	C 002:00D8:2
	WRITE(6,15)(AS(J),J=1,I+1)	C 002:00D8:2
15	FORMAT(1H0,10(F10.1,2X))	C 002:00E4:2
	SUM=0.	C 002:00E4:2
	SUMA=0.	C 002:00E5:0
C	CALCULATES MEAN AGE OF POST-RECRUIT POPULATION ASSUMING EQUILIBRIUM	C 002:00E5:4
C	CONDITIONS.TREATS AGE AT RECRUITMENT=1 YEAR,SO IF ACTUAL AGE AT	C 002:00E5:4
C	RECRUITMENT IS KNOWN TO BE T,ACTUAL MEAN AGE=GIVEN MEAN AGE+(T-1)	C 002:00E5:4
	DO 30 J=1,I+1	C 002:00E5:4
	TEMP=AS(J)	C 002:00E9:3
	SUM=TEMP*J+SUM	C 002:00EB:0
30	SUMA=TEMP+SUMA	C 002:00EC:3
	AGEB=SUM/SUMA	C 002:00EE:2
	WRITE(6,31)AGEB	C 002:00EF:4
31	FORMAT(5X,'MEAN AGE= ',F10.2)	C 002:00F6:2
	WRITE(6,16)	C 002:00F6:2
16	FORMAT(5X,'EQUILIBRIUM SIZE STRUCTURE')	C 002:00FA:2
	WRITE(6,15)(SS(I),I=1,N)	C 002:00FA:2
	SUM=0.	C 002:0106:2
	SUMA=0.	C 002:0107:0
C	CALCULATE MEAN LENGTH OF POST-RECRUIT POPULATION ASSUMING	C 002:0107:4
C	EQUILIBRIUM CONDITIONS	C 002:0107:4
	DO 32 I=1,N	C 002:0107:4
	C=(I-1)*SW+SW2	C 002:0109:0
	TEMP=SS(I)	C 002:010B:1
	SUM=TEMP*C+SUM	C 002:010C:4
32	SUMA=TEMP+SUMA	C 002:010E:1
	BLGT=SUM/SUMA	C 002:0111:4
	WRITE(6,33)BLGT	C 002:0113:0
33	FORMAT(5X,'MEAN LENGTH= ',F10.2)	C 002:0119:2
	WRITE(6,17)	C 002:0119:2
17	FORMAT(5X,'YIELD IN NUMBERS BY SIZE CLASS')	C 002:011D:2
	WRITE(6,15)(TOTY(I),I=1,N)	C 002:011D:2
C	CALCULATE YIELD IN WEIGHT FROM YIELD IN NUMBERS	C 002:0129:2
	DO 18 J=1,N	C 002:0129:2
	C=((J-1)*SW+SW2)*10.	C 002:012A:0
	TJ=TOTY(J)	C 002:012C:4
	YN=TJ*YW	C 002:012E:1
	IF(C.LT.40.)GO TO 25	C 002:012F:1
C	LENGTH-WEIGHT RELATIONSHIP	C 002:0130:3
	TJ=(26.0669-1.24*C+0.01535*C*C)*TJ	C 002:0130:3
	GO TO 26	C 002:0138:1
25	TJ=0.0255*C*TJ	C 002:0138:4
26	CONTINUE	C 002:013B:3
	TOTY(J)=TJ	C 002:013B:3
18	YW=TJ+YW	C 002:013D:1
	WRITE(6,19)	C 002:0140:4
19	FORMAT(5X,'YIELD IN WEIGHT BY SIZE CLASS')	C 002:0144:2
	WRITE(6,15)(TOTY(I),I=1,N)	C 002:0144:2
	WRITE(6,20)YN	C 002:0150:2
20	FORMAT(5X,'TOTAL YIELD IN NUMBERS= ',1PE18.6)	C 002:0157:2
	WRITE(6,21)YW	C 002:0157:2
21	FORMAT(5X,'TOTAL YIELD IN WEIGHT= ',1PE18.6)	C 002:015E:2
	DO 22 I=1,N	C 002:015E:2
	SS(I)=0.	C 002:015F:0
	TOTY(I)=0.	C 002:0160:3
22	POPVEC(I)=0.	C 002:0162:0
	YN=0.	C 002:0165:4
	YW=0.	C 002:0166:2
	GO TO 6	C 002:0167:0
999	STOP	C 002:0167:3
	END	C 002:0168:2
	002:016B:4 IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEMENT AT 002:0093	
	002:016E:5 IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEMENT AT 002:0085	
	SEGMENT 002 IS 0197 LONG	

	START OF SEGMENT 007	
	FORMAT SEGMENT IS 00C9 LONG	
C	SUBROUTINE PROB(J,GBAR,SG,IX,N,SW)	C 007:0000:0
C		C 007:0000:0
C	CALCULATES P(I,J) TERMS FROM INITIAL SIZE CLASS,SIZE CLASS WIDTH,	C 007:0000:0
C	MEAN AND VARIANCE OF LENGTH AT TIME T+1,THE DISTRIBUTION ASSUMED	C 007:0000:0
C	FOR THE GROWTH IS CONTAINED IN SUBROUTINE PROBN.	C 007:0000:0
C		C 007:0000:0
	COMMON/GROW/P(200,200)	C 007:0000:0
	REAL L	C 007:0000:0
	L=J*SW	C 007:0000:0
	TEMPL=PROBN(L,GBAR,SG)	C 007:0001:2
	P(J,J)=TEMPL	C 007:0004:0
	IF(J.EQ.N)GO TO 2	C 007:0006:5

```

DO 1 I=J+1,N
L=L+SW
TEMPU=PROBN(L,GBAR,SG)
P(I,J)=TEMPU-TEMPL
1 TEMPL=TEMPU
2 IF(TEMPL.EQ.1)RETURN
WRITE(6,4)
4 FORMAT(/)
WRITE(6,3)J,TEMPL
3 FORMAT(10X,'SUM OF P FOR CLASS',I3,'IS',F10.8,/,10X,
1'CHECK GROWTH FUNCTION')
P(N,J)=P(N,J)+1,-TEMPL
C IF PROGRAM IS TO TERMINATE WHEN GROWTH FUNCTION IS NOT TOTALLY
C CONTAINED WITHIN MATRIX(COMMON,ALTHOUGH USUALLY NEGLIGIBLE IF
C GROWTH INCREMENT IS TREATED AS NORMALLY DISTRIBUTED)THE FOLLOWING
C CARD SHOULD BE INCLUDED;
C IYX=1
C RETURN
END

```

```

C 007:0008:1
C 007:000A:0
C 007:000B:2
C 007:000E:0
C 007:0011:2
C 007:0014:2
C 007:0015:3
C 007:0019:2
C 007:0019:2
C 007:0021:2
C 007:0021:2
C 007:0025:0
C 007:0025:0
C 007:0025:0
C 007:0025:0
C 007:0025:0
C 007:0025:0
C 007:0025:0
C 007:0025:3
SEGMENT 007 IS 0033 LONG

```

```

SUBROUTINE ZLOAD(NN)
C LOADS SIZE CLASS PROJECTION MATRIX(EXCEPT RECRUITMENT TERMS) USING G
C SIZE SPECIFIC NATURAL AND FISHING MORTALITIES AND THE P(I,J) TERMS
C CALCULATED IN SUBROUTINE PROB
C
COMMON/GROW/P(200,200)
COMMON/MAT/Z(200,200)
COMMON/MORT/MORTP(200),MORTQ(200)
REAL MPAI,M01,MORTP,MORTQ
T=1.
DO 2 I=1,NN
M01=MORTP(I)
P1=P(I,1)
MPAI=MORTP(I)+MORTQ(I)
Z(I,1)=P1*EXP(-MPAI*T)
IF(I.EQ.NN)GO TO 2
DO 3 J=1+1,NN
TEMEX=0.
Z(J,1)=0.
IF(P(J,1).EQ.0.)GO TO 3
TJ1=T/(2*(J-1))
TTJ1=2*TJ1
TEMEX=MPAI*TJ1
IF(J.EQ.1+1)GO TO 178
DO 44 K=1+1,J-1
44 TEMEX=((MORTP(K)+MORTQ(K))*TTJ1)+TEMEX
178 CONTINUE
TEMEX=((MORTP(J)+MORTQ(J))*TJ1)+TEMEX
3 Z(J,1)=P(J,1)*EXP(-TEMEX)
2 CONTINUE
RETURN
END

```

```

START OF SEGMENT 008
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:0
C 008:0000:4
C 008:0002:0
C 008:0003:3
C 008:0006:1
C 008:0009:0
C 008:0000:4
C 008:000F:0
C 008:0011:0
C 008:0011:4
C 008:0014:2
C 008:0017:2
C 008:0019:4
C 008:001B:0
C 008:001C:2
C 008:001E:0
C 008:0022:3
C 008:0026:5
C 008:0026:5
C 008:002A:4
C 008:0030:4
C 008:0032:5
C 008:0035:0
C 008:0035:3
SEGMENT 008 IS 0030 LONG

```

```

FUNCTION PROBN(Y,YBAR,S)
C CALCULATES THE PROBABILITY OF LENGTH BEING LESS THAN OR EQUAL
C TO Y FROM THE MEAN AND STANDARD DEVIATION OF LENGTH AT TIME
C T+1 FOR A NORMAL DISTRIBUTION
C
Z=(Y-YBAR)/S
X=ABS(Z)
T=1./(1.+0.2316419*X)
PROBN=1.-0.3989423*EXP(-X*X/2.)*T*(0.31938153+T*(-.35656378+T*(1.7
18147794+T*(-1.82125598+T*1.330227443))))
IF(Z) 5,10,10
5 PROBN=1.-PROBN
10 RETURN
END

```

```

START OF SEGMENT 00A
C 00A:0000:0
C 00A:0000:0
C 00A:0000:0
C 00A:0000:0
C 00A:0000:0
C 00A:0000:0
C 00A:0001:5
C 00A:0002:4
C 00A:0006:2
C 00A:000E:3
C 00A:0016:1
C 00A:0017:2
C 00A:0018:3
C 00A:0019:0
SEGMENT 00A IS 0021 LONG

```

	SUBROUTINE GEN(POPVEC,YIELD,DEN,NN)	START OF SEGMENT 00B
C		C 00B:0000:0
C	CALCULATES THE POPULATION VECTOR(POPVEC) AT T+1 GIVEN THE POPULATI ON	C 00B:0000:0
C	VECTOR AT T AND THE PROJECTION MATRIX.CALCULATES THE YIELD	C 00B:0000:0
C	OBTAINED DURING THIS PERIOD AND THE TOTAL NUMBER OF ANIMALS	C 00B:0000:0
C	PRESENT AT THE END OF THE PERIOD	C 00B:0000:0
C	INPUT POPVEC(T)	C 00B:0000:0
C	OUTPUT POPVEC(T+1),YIELD(T TO T+1), SUM OF POPVEC(T+1)	C 00B:0000:0
C		C 00B:0000:0
	COMMON/GROW/P(200,200)	C 00B:0000:0
	COMMON/MAT/Z(200,200)	C 00B:0000:0
	COMMON/MORT/MORTP(200),MORTQ(200)	C 00B:0000:0
	DIMENSION POPVEC(200),YIELD(200)	C 00B:0000:0
	DIMENSION TEMVEC(200)	C 00B:0000:0
	REAL MORTP,MORTQ,MOI,MPAI,MPAK,MJ,MPAJ	C 00B:0000:0
	T=1.	C 00B:0000:0
	DO 100 I=1,NN	C 00B:0000:4
	FTEST=FTEST+MORTP(I)	C 00B:0002:0
100	YIELD(I)=0.	C 00B:0004:0
C	IF THERE IS NO FISHING MORTALITY SKIP YIELD CALCULATIONS	C 00B:0008:1
	IF(FTEST.EQ.0.)GO TO 51	C 00B:0008:1
	DO 2 I=1,NN	C 00B:0009:2
	MOI=MORTP(I)	C 00B:000A:0
	PI=P(I,I)	C 00B:000B:3
	POI=POPVEC(I)	C 00B:000E:1
	MPAI=MORTP(I)+MORTQ(I)	C 00B:0010:1
	YIELD(I)=((MOI*POI*PI*(1-(EXP(-MPAI*T))))/MPAI)+YIELD(I)	C 00B:0013:0
	IF(I.EQ.NN)GO TO 2	C 00B:0019:2
	DO 133 J=I+1,NN	C 00B:001A:4
	PJ=P(J,I)	C 00B:001C:0
	TEMEX=0.	C 00B:001E:4
	IF(PJ.EQ.0.)GO TO 133	C 00B:001F:2
	TJI=T/(2*(J-I))	C 00B:0020:3
	TTJI=2*TJI	C 00B:0022:5
	YIELD(I)=(MOI*POI*PJ*(1-EXP(-MPAI*TJI)))/MPAI+YIELD(I)	C 00B:0024:1
	TEMEX=MPAI*TJI +TEMEX	C 00B:002A:3
	IF(J.EQ.I+1)GO TO 155	C 00B:002C:2
	DO 144 K=I+1,J-1	C 00B:002E:0
	PK=MORTP(K)	C 00B:0032:3
	MPAK=PK+MORTQ(K)	C 00B:0034:0
	YIELD(K)=((PK*POI*PJ*EXP(-TEMEX)*(1-EXP(-MPAK*TTJI)))/MPAK)+	C 00B:0035:5
	YIELD(K)	C 00B:003C:5
144	TEMEX=(MPAK*TTJI)+TEMEX	C 00B:003D:3
155	CONTINUE	C 00B:003F:5
	MJ=MORTP(J)	C 00B:003F:5
	MPAJ=MJ+MORTQ(J)	C 00B:0041:2
	YIELD(J)=((MJ*POI*PJ*EXP(-TEMEX)*(1-EXP(-MPAJ*TJI)))/MPAJ)+	C 00B:0043:1
	YIELD(J)	C 00B:004A:1
133	CONTINUE	C 00B:004A:5
2	CONTINUE	C 00B:0040:0
51	CONTINUE	C 00B:004F:1
	DO 15 I=1,NN	C 00B:004F:1
	PI=POPVEC(I)	C 00B:0050:0
	DO 15 K=1,NN	C 00B:0052:0
15	TEMVEC(K)=(Z(K,I)*PI)+TEMVEC(K)	C 00B:0053:0
	DO 52 I=1,NN	C 00B:005B:5
	DEN=DEN+TEMVEC(I)	C 00B:005D:0
	POPVEC(I)=TEMVEC(I)	C 00B:005F:0
52	TEMVEC(I)=0.	C 00B:0061:5
	RETURN	C 00B:0065:3
	END	C 00B:0066:0
		SEGMENT 00B IS 006F LONG

FORMAT SEGMENT IS 0012 LONG  
 START OF SEGMENT 00C  
 SEGMENT 00C IS 002F LONG

NO ERRORS DETECTED. NUMBER OF CARDS = 304.  
 COMPILATION TIME = 19 SECONDS ELAPSED. 3.90 SECONDS PROCESSING.  
 D2 STACK SIZE = 26 WORDS. FILESIZE = 140 WORDS. ESTIMATED CORE STORAGE REQUIREMENT = 4354 WORDS.  
 TOTAL PROGRAM CODE = 781 WORDS. ARRAY STORAGE = 3350 WORDS.  
 NUMBER OF PROGRAM SEGMENTS = 13. NUMBER OF DISK SEGMENTS = 68.  
 PROGRAM CODE FILE = (Z00L033)SCYPR ON PACK, COMPILER COMPILED ON 01/31/77(FORTRAN ON PACK)

YIELD PER RECRUITMENT ANALYSIS USING SIZE CLASS POPULATION MODEL, ALL CALCULATIONS BASED ON 1000.0 RECRUITS  
WITH THE FOLLOWING GROWTH PARAMETERS

L INFINITY= 13.19000  
VARIANCE OF L INFINITY= 1.38700  
K= 0.16360  
VARIANCE OF K= 0.01180

SUM OF P FOR CLASS 14 IS 0.99999875  
CHECK GROWTH FUNCTION

SUM OF P FOR CLASS 15 IS 0.97176006  
CHECK GROWTH FUNCTION

MIN. LEGAL SIZE=80MM; F=0.1; M=0.1 FOR ALL SIZE CLASSES

EQUILIBRIUM AGE STRUCTURE (IN YEAR CLASSES)									
1000.0	904.7	812.0	709.0	600.9	499.8	411.8	338.0	277.0	226.9
185.8	152.1	124.5	101.9	83.5	68.3	56.0	45.8	37.5	30.7
25.1	20.6	16.9	13.8	11.3	9.2				
MEAN AGE= 5.77									
EQUILIBRIUM SIZE STRUCTURE									
0.0	0.0	0.0	170.2	908.1	485.8	698.8	825.0	819.2	783.7
739.8	661.8	469.4	168.1	33.2					
MEAN LENGTH= 8.35									
YIELD IN NUMBERS BY SIZE CLASS									
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	81.4	77.8
73.6	66.1	46.9	16.6	3.2					
YIELD IN WEIGHT BY SIZE CLASS									
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2569.4	3639.7
4789.2	5712.8	5197.0	2302.4	544.5					
TOTAL YIELD IN NUMBERS=				3.655006E+02					
TOTAL YIELD IN WEIGHT=				2.475499E+04					